

Ex libris universitates albertheasis













Elements of Biology



e- Euri QH 308.5 W43

ELEMENTS OF BIOLOGY

Paul B. Weisz

PROFESSOR OF BIOLOGY BROWN UNIVERSITY

McGRAW-HILL Company of Canada, Limited
NEW YORK TORONTO LONDON

ELEMENTS OF BIOLOGY

Canadian Edition

Copyright © 1963 by McGraw-Hill Company of Canada Limited. $94523 \label{eq:copyright}$



This book is set in Linotype Baskerville, a type face based on the original designs of the eighteenth-century English printer and type founder John Baskerville. The chapter titles are Bulmer and the displayed heads Alternate Gothic.

UNIVERSITY
OF ALBERTA LIBRARY

Kin Ser D

PREFACE

The Elements of Biology has been prepared with the conviction that a beginning course in biology should be analytical rather than merely descriptive. Instead of being an exercise in memorization, the course should convey understanding of some of the principles underlying living phenomena. Furthermore, the basic morphological unit of discussion might profitably be the molecule, with the basic physiological unit being the molecular reaction. One of the important aims should be to show, in so far as this can be shown, how the various microscopic and macroscopic attributes of living organisms ultimately result from molecules and their interactions.

A course of this kind need not necessarily delve deeply into details of actual chemistry. It is important only that the general *orientation* be molecular; the student should learn to think about living processes "from the molecule up," as it were. Where desired, of course, the conceptual framework may be augmented with as little or as much chemical detail as the student can profitably absorb. But the first essential is to provide at least the molecular conceptual framework. This in itself does not make a course any more advanced or more difficult than a traditional presentation. On the contrary, because it probes deeply and searches for molecular foun-

dations, it makes the traditional far more meaningful and more satisfyingly comprehensible.

Elements of Biology has been written with this in mind: to permit a minimum but adequate presentation of the molecularly oriented conception of biology, even in the most basic courses. The organizational attributes of living matter are examined in the first two parts of this book. Ranging over the whole biological domain, Part One discusses the origin of life, and in sequence from atom and molecule up, the nature of all major levels of living organization. These chapters are the key to the molecular orientation.

Part Two deals with the nature and structure of the living substance. A chapter on protoplasmic properties and cellular organization is followed by accounts of the types of living organisms and their design. These sections also introduce a four-part classification of organisms into Monera, Protista, Metaphyta, and Metazoa. Based on ample biochemical and cytological data and on critical discussions in recent literature, such a scheme substantially improves on the now too simple subdivision of the living world into merely "plants" and "animals."

The operational attributes of living matter are dealt with in the remaining four parts of the book. Part Three is a thoroughly up-to-date account of

metabolism. Oversimplification is avoided here, but only a minimum amount of chemical detail is presented. For example, in the sections on photosynthesis and respiration all the important reaction sequences are discussed (with the aid of newly devised, clear flow diagrams). But the detailed chemical formulas and equations ordinarily required for a more comprehensive discussion are omitted. Similarly, elsewhere, important modern concepts are presented fully in depth but their elaboration in breadth is kept to a minimum.

Parts Four, Five, and Six deal with self-perpetuation. Under the headings of steady-state control, reproduction, and adaptation, these concluding portions examine the living functions based on metabolism. As elsewhere, the presentation is oriented toward analysis, while the descriptive narrative carries the burden of elucidating the basic principles involved.

It has become fashionable in extolling the merits of college textbooks to say (among other things) that they admirably fulfill the requirements of both one-semester and two-semester courses, are equally suitable for both majors and nonmajors, are not

overly difficult for dull students yet challenging to the bright ones, and are compatible with the teaching philosophy of yesteryear as well as today and tomorrow. Such claims are perhaps helpful in dispelling prejudice against the merits of the texts but they tend to perpetuate the fiction that one textbook can be all things to all people. The truth is somewhat less spectacular; a new textbook can be a genuine aid to the instructor in teaching the kind of course he wants to teach, provided the textbook comes reasonably close to the instructor's idea of what should be covered and how presented. Thus, if a text approximates the idea and is written within a reasonably logical framework and if consideration is given to the problems involved in changing the chapter sequence, then the means of adapting a text to individual needs are available. Beyond that, general claims are meaningless. Accordingly, if Elements of Biology can serve as a satisfactory approximation of a teacher's ideal course plan, then its preparation will have been worth the effort.

Paul B. Weisz

CONTENTS

Preface v

3 CELL AND ORGANISM

HE NATURE OF SCIENCE			Page
The Origin of Science			
The Forms of Science			
The Procedure of Science	Observation	Problem	Hypothesis
Experiment Theory			
The Limitations of Science	The scientif	ic domain	
The scientific aim Scien	ice and values	Science a	nd purposes
The Language of Science	Science as a w	hole Biol	ogy

Part One THE LIVING WORLD

2	THE ORIGIN OF LIFE			Page	17
	The Chemical Backgrou	and Atoms and	l molecules		
	Molecules and reac	tions			
	Chemical Evolution	The early earth	The first round		
	The second round	The third round	The fourth round	l	
	Biological Evolution	The fifth round	The sixth round		
	The seventh round				

Functional Characteristics
Structural Characteristics
Results of aggregation

Levels of organization
Specialization

Page 43

4	SPECIES AND COMMUNITY	Page	54
	The Species The nature of a species Variations The Society Insect societies Vertebrate societies The Community Cycles and balances Control factors Symbiosis The pattern Parasitism		
5	COMMUNITY AND ENVIRONMENT	Page	75
	The Communal Habitats The oceanic habitat The fresh-water habitat The Global Environment Geochemical cycles		
	Part Two		
	THE LIVING ORGANIZATION		
6	PROTOPLASM AND CELLS	Page	95
	The Composition of Protoplasm The inorganic compo- The organic components The Properties of Protoplasm Ionization Enzymes The colloidal state Protoplasmic membranes Osmos The Structure of Protoplasm Fundamental structure Nucleus and cytoplasm The cell surface		
7	MONERA AND PROTISTA	Page	119
	Kinds of Organisms Methods of classification The main groups of organisms The Monera The Protista Algae Protozoa Slime molds Fungi		
8	METAPHYTA: ADVANCED PLANTS	Page	143
	Bryophytes Tracheophytes Patterns of Life Internal Structure Stems: herbaceous types Stems: woody types Roots Leaves		

Animal Characteristics Nutrition and movement Animal structure Radiata Sponges Coelenterates Page 163

9 METAZOA: ADVANCED ANIMALS

Acoelomates Flatworms

Pseudocoelomates Rotifers Roundworms

Schizocoelomates Mollusks Segmented worms Arthropods

Echinoderms Chordates Enterocoelomates

Part Three METABOLISM

AUTOTROPHIC NUTRITION

Page 197

Autotrophic Patterns

The Inorganic Nutrients Soil Absorption

Internal Transport Xylem conduction Phloem conduction Chloroplasts and chlorophyll Light and water Photosynthesis | PGHIL

CO, fixation The endproduct

HETEROTROPHIC NUTRITION

Page 216

Heterotrophic Patterns Ingestion and Digestion Absorption and Egestion The Transport Pathways Liver Function

Ingestion: hunger Digestion: enzymes

Paral sold sold sold

GAS EXCHANGE

Page 233

Patterns of Breathing The Breathing System Structural components The breathing process The control of breathing Gas Transport The exchanges The vehicle Pulmerens respirit.

CELLULAR METABOLISM: RESPIRATION

Page 246

The Pattern of Respiration Bonds and energy Oxidation The fuels The energy gain The pattern The process Energy Transfer Hydrogen Transfer Aerobic respiration Anaerobic respiration Fuel Combustion The pattern Carbohydrate breakdown C_3 to C_1 The general result

CELLULAR METABOLISM: ENERGY UTILIZATION

Page 264

Physical Uses of Energy Movement Heat production Bioluminescence Bioelectricity Chemical Uses of Energy Synthesis patterns Protein synthesis Other syntheses

Part Four

SELF-PERPETUATION: THE STEADY STATE

A 15 THE PATTERN OF CONTROL

Page 277

Principles of Control Components of control systems
Properties of control systems
Protoplasmic Controls Molecular control
Supramolecular control

16 CELLULAR CONTROLS

Page 287

Genes Structure Function Consequences of gene function Vitamins and Hormones Vitamins Plant hormones

Animal hormones p301 - 1

17 THE BODY FLUIDS

Page 303

Blood and Lymph Blood plasma Blood cells Blood Table F303

Circulation The pathway The process The control

Excretion Kidney structure Kidney function

18 NERVOUS COORDINATION

Page 320

The Neural Pathways
Nerve cells Reflex arcs
Nerve impulses

The Neural Receptors
Dispersed receptors Taste and smell

Vision The ear

The Neural Centers Structural features Functional features

Part Five SELF-PERPETUATION: REPRODUCTION

19 THE PATTERN OF REPRODUCTION

Page 349

Molecular and Cellular Reproduction The patterns
Mitotic division
Organismic Reproduction The patterns Sexuality Meiosis

20 REPRODUCTION: MONERA, PROTISTA, METAPHYTA

Page 371

Monera
Protista Algae Fungi Protozoa
Metaphyta Bryophyte reproduction
Tracheophyte reproduction

21	REPRODUCTION: METAZOA	Page	392
	Reproductive Patterns The Gametes Reproductive systems Menstrual cycles The Embryo Development Embryo and environment		
	Part Six		
	SELF-PERPETUATION: ADAPTATION		
22	HEREDITY	Page	411
	Genes and Traits		
	Mendelian Inheritance The chromosome theory The law of segregation The law of independent assor The law of linear order Non-Mendelian Inheritance Gene-gene interactions Inheritance of sex Transduction and transformation Mutation	tment	
23	THE MECHANISM OF EVOLUTION	Page	429
	Background Lamarck Darwin and Wallace The Forces of Evolution The evolutionary process The genetic basis The Nature of Evolution Speciation Characteristics of evolution		
24	THE COURSE OF EVOLUTION	Page	446
	The First Three Quarters Geologic time The pre-Cambrian era The Last Quarter The Paleozoic The Mesozoic and C The Evolution of Man The primate background The prehuman line Modern man	enozo	ic
	GLOSSARY	Page	471
	INDEX	Page	485



Elements of Biology



CHAPTER 1

The nature of science

ur current civilization is so thoroughly permeated with science that, for many, the label "scientific" has become the highest badge of merit, the hallmark of progress, the dominant theme of the age of atoms and space. No human endeavor, so it is often claimed, can really be worthwhile or of basic significance unless it has a scientific foundation. Moreover, advertisements loudly proclaim the "scientific" nature of consumer goods, and their "scientifically proved" high quality is attested to by "scientific" experts. Human relations too are supposed to be "scientific" nowadays. Conversation and debate have become "scientific" discussions,

and in a field such as sports, if one is a good athlete, he is a "scientific" athlete.

There are even those who claim to take their religion "scientifically" and those who stoutly maintain that literature, painting, and other artistic pursuits are reducible to "science," really. And then there are those who believe that science will eventually solve "everything" and that, if only the world were run more "scientifically," it would be a much better place.

Yet in contrast to this widespread confidence in things and activities which claim to be, and in a few cases actually are, scientific, large segments of 2

society doubt and mistrust scientists as persons. To many, the scientist is somehow queer and "different." He is held to be naive and more or less uninformed outside his specialty. He is pictured as a cold, godless calculating machine, living in a strange, illusory world of his own.

Many circumstances in our civilization conspire to foster such false, stereotyped notions about science and scientists. However, no one who wishes to consider himself properly educated can afford to know about the meaning of science only what popular misconceptions and "common knowledge" may have taught him. Especially is this true for one who is about to pursue studies in a modern science such as biology.

What then is the actual meaning of science? How did truly scientific undertakings develop, and how does science "work"? What can it do, and more especially, what can it not do? How does science differ from other forms of activity, and what place does it have in the scheme of modern culture?

THE ORIGIN OF SCIENCE

Science began in the distant past, long before human history was being recorded. Its mother was tribal *magic*.

The same mother also gave birth to religion and, probably even earlier, to art. Thus science, religion, and art have always been blood brothers. Their methods differ, but their aim is the same: to understand and interpret the universe and its working and, from this, to promote the material and spiritual welfare of man, where possible.

This was also the function of tribal magic. For long ages, magic was the rallying point of society, the central institution in which were concentrated the accumulated wisdom and experience of the day. The execution of magical procedures was in the hands of specially trained individuals, the medicine men and their equivalents. These were the forerunners of the scientists and the clergymen of today. How did science and religion grow out of magic? We may illustrate by means of an example.

Several thousand years ago, it was generally be-

lieved that magical rites were necessary to make wheat grow from planted seeds. In this particular instance, the rites took one of two forms. Either man intensified his sexual activity, in a solemn spring festival celebrated communally in the fields, or he abstained completely from sexual activity during the planting period.

The first procedure was an instance of *imitative* magic. The reasoning was that since sowing seeds is like producing pregnancy in a woman, man could demonstrate to the soil what was wanted and so induce it to imitate man and be fertile. The second procedure, an instance of *contagious* magic, grew out of the assumption that only a limited amount of reproductive potency was available to living things. Consequently, if man did not use up his potency, that much more would become available for the soil. Depending on the tribe, the time, and the locality, either imitative or contagious magic might have been used to attain the same end, namely, to make the earth fruitful.

The fundamental weakness of magic was, of course, that it was unreliable. Sometimes it worked, and sometimes it did not work. Bad soil, bad grain, bad weather, and insect pests often must have defeated the best magic. In time, man must have realized that magical rites actually played no role in wheat growth, whereas soil conditions, grain quality, and good weather played very important roles. This was a momentous discovery—and a scientific one.

Magic became science when man accidentally found, or began to look for, situations which could be predictably controlled without magical rituals. In many situations where magic seemed to work successfully most of the time, man discovered an underlying scientific principle.

Yet there remained very many situations where magic did not work and where scientific principles could not be found. For example, in spite of good soil and good weather, wheat might not have grown because of virus or fungus infections. Such contingencies remained completely beyond understanding up to very modern times, and early man could only conclude that unseeable, uncontrollable

"somethings" occasionally defeated his efforts. These somethings became spirits and gods. And unless prayers and sacrificial offerings maintained the good will of the gods, their wrath would undo human enterprise. Thus magical rituals evolved into primitively religious ones.

At this stage, medicine men ceased to be magicians and instead assumed the dual role of priest and scientist. Every personal or communal undertaking required both scientific and religious action: science to put to use what was known; religion, to protect against possible failure by inducing the unknown to work on man's side.

In time, the "two-way" medicine man disappeared and made way for the specialized scientist and priest. In both religion and science, shades of the old magic lingered on for long periods. The religions still retain a high magical content today, and the sciences only recently dissociated from magic-derived pseudosciences such as alchemy, astrology, and the occult arts.

Throughout the early development of science and religion, emphasis was largely on practical matters. Science was primitively technological, and religion too was largely "applied," designed to deal with the concrete practical issues of the day. Man was preoccupied mainly with procuring food, shelter, and clothing, and science and religion served these necessities. Later, as a result of technological successes, more time became available for contemplation and cultural development, and this is when researchers and theorists appeared alongside the technologists, and theologians alongside the clergymen.

THE FORMS OF SCIENCE

Today there are three types of scientists carrying on two kinds of science.

One kind of scientist may be symbolized as a man who sits by the river on nice afternoons and who whittles away at a stick and wonders about things. Strange as it may seem to some, the most powerful science stems from such whittlers. Whereas most people who just sit manage merely to be lazy, a few quietly boil with rare powers and make the wheels

of the world go round. Thinker-scientists of this sort usually are not too well known by the general public, unless their thoughts prove to be of outstanding importance. Newton, Einstein, Darwin, and Freud are among the best known.

A second kind of scientist is the serious young man in the white coat, reading the dials of monster machines while lights flash and buzzers purr softly. This picture symbolizes the technician, the lab man, the trained expert who tests, experiments, and works out the implications of what the whittler has been thinking.

The third kind of scientist is a relatively new phenomenon. He goes to an office, dictates to secretaries, and spends a good part of his time in conferences or in handling contracts, budgets, and personnel. This symbolizes the businessman-scientist, who gets and allocates the funds which buy time and privacy for the whittler and machines for the lab man.

Note, however, that every scientist worthy of the name actually is a complex mixture of philosopher, technician, and businessman all rolled into one, and none is a "pure" type. But the relative emphasis varies greatly in different scientists.

Whatever type mixture he may be, a scientist works either in basic research, often called <u>pure science</u>, or in technology, often called <u>applied science</u>.

Basic research is done primarily to further man's understanding of nature. Possible practical applications of the findings are here completely disregarded. Scientists in this field are more frequently of the philosopher-lab-man type than in technology. They may be found principally in university laboratories and research institutes and, in lesser numbers, in industry and government. They have little to show for their efforts beyond the written accounts of their work; hence it is comparatively hard for them to convince nonscientists that they are doing anything essential. However, government and enlightened industry today support independent research or conduct such research. And the public is beginning to realize that pure science is the soil from which applied science must develop.

4 THE NATURE OF SCIENCE

Technology is concerned primarily with applying the results of pure science to practical uses. No lesser inventiveness and genius are required in this field than in basic research, though here the genius is more of a commercial and less of a philosophical nature. Physicians, engineers, crime detectives, drug manufacturers, agricultural scientists, all are technologists. They have services and tangible products to sell; hence the public recognizes their worth rather readily.

Here again, note that no scientist is pure researcher or pure technologist. Mixtures are in evidence once more, with emphasis one way or the other. Moreover, technology is as much the fertilizer of basic research as the other way round. As new theories suggest new ways of applying them, so new ideas for doing things suggest further advances in research. Thus, in most research today, pure and applied science work hand in hand. Many conclusions of pure science cannot be tested before the technologist thinks up the means of testing. Conversely, before the technologist can produce desirable new products, years of basic research may first be required. In so far as every basic researcher must use equipment, however modest, he is also a technologist; and in so far as every technologist must understand how and why his products work, he is also a basic researcher.

It follows that any science shrivels whenever either of its two branches ceases to be effective. If for every dollar spent on science an immediate, tangible return is expected, and if the budding scientist is prevented from being a whittler by the necessity of producing something salable, then basic research will be in danger of drying up. And when that happens, technology too will become obsolete.

THE PROCEDURE OF SCIENCE

Everything that is science ultimately has its basis in the scientific method. Both the powers and the limitations of science are defined by this method. And wherever the scientific method cannot be applied, there cannot be science.

Taken singly, most of the steps of the scientific

method involve commonplace procedures carried out daily by every person. Taken together, they amount to the most powerful tool man has devised to know and to control nature.

Observation

All science begins with observation, the first step of the scientific method.

At once this delimits the scientific domain; something that cannot be observed cannot be investigated by science. However, observation need not be direct. Atomic nuclei, for example, or magnetism cannot be perceived directly through our sense organs. But their effects can be observed with instruments. Similarly, mind cannot be observed directly, but its effects can be, as expressed, for example, in behavior.

For reasons which will become clear presently, it is necessary, furthermore, that an observation be repeatable, actually or potentially. Anyone who doubts that objects fall back to the ground after being thrown into the air can convince himself of it by repeating the observation. One-time events on earth are outside science.

Correct observation is a most difficult art, acquired only after long experience and many errors. Everybody observes, with eyes, ears, touch, and all other senses, but few observe correctly. Lawyers experienced with witnesses, artists who teach students to draw objects in plain view, and scientists who try to see nature, all can testify to this.

This difficulty of observation lies largely in unsuspected bias. People forever see what they want to see, or what they think they ought to see. It is extremely hard to rid oneself of such unconscious prejudice and to see just what is actually there, no more and no less. Past experience, "common knowledge," and often teachers can be subtle obstacles to correct observation, and even experienced scientists may not always avoid them. That is why a scientific observation is not taken at face value until several scientists have repeated the observation independently and have reported the same thing. That is also a major reason why one-time, unrepeatable events normally cannot be science.

A scientific piece of work is only as good as the original observation. Observational errors persist into everything that follows, and the effort may be defeated before it has properly begun.

Problem

After an observation has been made, the second step of the scientific method is to define a *problem*.

In other words, one asks a question about the observation. How does so and so come about? What is it that makes such and such happen in this or that fashion? Question asking additionally distinguishes the scientist from the layman; everybody makes observations, but not everybody shows further curiosity.

More significantly, not everyone sees that there may actually be a problem connected with an observation. During thousands of years, even curious people simply took it for granted that a detached, unsupported object falls to the ground. It took genius to ask "How come?" and few problems, indeed, have ever turned out to be more profound.

Thus scientists take nothing for granted, and they ask questions, even at the risk of irritating others. Question askers are notorious for getting themselves into trouble, and so it has always been with scientists. But they have to continue to ask questions if they are to remain scientists. And society has to expect annoying questions if it wishes to have science.

Anyone can ask questions. However, good questioning, like good observing, is a high art. To be valuable scientifically, a question must be *relevant* and it must be *testable*. The difficulty is that it is often very hard or impossible to tell in advance whether a question is relevant or irrelevant, testable or untestable. If a man collapses on the street and passers-by want to help him, it may or may not be irrelevant to ask when he had his last meal. Without experience one cannot decide on the relevance of this question, and wrong procedure might be followed.

As to the testability of questions, it is clear that proper testing techniques must be available, actually or potentially. This cannot always be guar-

anteed. For example, Einstein's fame rests, in part, on showing that it is impossible to test whether or not the earth moves through an "ether," an assumption held for many decades. All questions about an ether therefore become nonscientific, and we must reformulate associated problems until they become testable. Einstein did this, and he came up with relativity.

In general, science does best with "How?" or "What?" questions. "Why?" questions are more troublesome. Some of them can be rephrased to ask "How?" or "What?" But others such as "Why does the universe exist?" fall into the untestable category. These are outside the domain of science.

Hypothesis

Having asked a proper question, the scientist proceeds to the third step of the scientific method. This involves the seemingly quite unscientific procedure of guessing. One guesses what the answer to the question might conceivably be. Scientists call this postulating a *hypothesis*.

Hypothesizing distinguishes the scientist still further from the layman. For while many people observe and ask questions, most stop there. Some do wonder about likely answers, and scientists are among these.

Of course, a given question may have thousands of *possible* answers but only one *right* answer. Chances are therefore excellent that a random guess will be wrong. The scientist will not know whether his guess was or was not correct until he has completed the fourth step of the scientific method, *experimentation*. It is the function of every experiment to test the validity of a scientific guess.

If experimentation shows that the first guess was wrong, the scientist then must formulate a new hypothesis and once more test for validity by performing new experiments. Clearly, the guessing and guess testing might go on for years, and a right answer might never be found. This happens.

But here again, artistry, genius, and experience usually provide shortcuts. There are good guesses and bad ones, and the skilled scientist is generally able to decide at the outset that, of a multitude of possible answers, so and so many are unlikely answers. His knowledge of the field, his past experience, and the experience of others working on related problems normally allow him to reduce the many possibilities to a few likelihoods.

This is also the place where hunches, intuitions, and lucky accidents aid science enormously. In one famous case, so the story has it, the German chemist Kekule went to bed one night after a fairly alcoholic party and dreamed of six monkeys chasing one another in a circle, the tail of one held in the teeth of the other. Practically our whole chemical industry is based on that dream, for it told the sleeping scientist what the long-sought structure of benzene was—as we now know, six carbon atoms "chasing" one another in a circle. And benzene is the fundamental parent substance for thousands of chemical products.

The ideal situation for which the scientist generally strives is to reduce his problem to just two distinct alternative possibilities, one of which, when tested by experiment, may then be answered with a clear "Yes," the other with a clear "No." It is exceedingly difficult to streamline problems in this way, and with many it cannot be done. Very often the answer obtained is "Maybe." However, if a clear "Yes" or "No" does emerge, scientists speak of an elegant piece of work, and such performances often are milestones in science.

Experiment

Experimentation is the fourth step in the scientific method. At this point, science and nonscience finally and completely part company.

Most people observe, ask questions, and also guess at answers. But the layman stops here: "My answer is so logical, so reasonable, and it sounds so 'right' that it must be correct." The listener considers the argument, finds that it is indeed logical and reasonable, and is convinced. He then goes out and in his turn converts others. Before long, the whole world rejoices that it has the answer.

Now the small, kill-joy voice of the scientist is heard in the background: "Where is the evidence?"

Under such conditions in history, it has often been easier and more convenient to eradicate the scientist than to eradicate an emotionally fixed public opinion. But doing away with the scientist does not alter the fact that answers without evidence are at best unsupported opinions, at worst wishful thinking and fanatical illusions. Experimentation can provide the necessary evidence, and whosoever then experiments after guessing at answers becomes truly "scientific" in his approach, be he a professional scientist or not.

On the other hand, experiments do not guarantee a scientific conclusion. For there is ample room within experimentation and in succeeding steps to become unscientific again.

Experimentation is by far the hardest part of scientific procedure. There are no rules to follow; each experiment is a case unto itself. Knowledge and experience usually help technically, but to design the experiment, to decide on the means by which a hypothesis might be tested, that separates the genius from the dilettante. The following example will illustrate the point:

Suppose that you observe that a chemical substance X, which has accidentally spilled into a culture dish full of certain disease-causing bacteria, kills all the bacteria in that dish. Problem: can drug X be used to protect human beings against these disease-causing bacteria? Hypothesis: yes. Experiment: you go to a hospital and find a patient with that particular bacterial disease and inject some of the drug into the patient.

Possible result no. 1: two days later the patient is well. Conclusion: hypothesis confirmed. You proceed to market the drug at high prices. Shortly afterward, users of the drug die by the dozens, and you are tried and convicted for homicide.

Possible result no. 2: two days later the patient is dead. Conclusion: the drug is worthless, and you abandon your project. A year later a colleague of yours is awarded the Nobel prize for having discovered a drug X which cures a certain bacterial disease in man—the same drug and the same disease in which you had been interested.

In this example, the so-called experiment was not an experiment at all.

First, no allowance was made for the possibility that people of different age, sex, eating habits, prior medical history, hereditary background, etc., might react differently to the same drug. Obviously, one would have to test the drug on many categories of carefully preselected patients, and there would have to be many patients in each such category. Besides, one would make the tests first on mice, or guinea pigs, or monkeys.

Second, the quantity of drug to be used was not determined. Clearly, a full range of dosages would have to be tested, for each different category of patient. We tacitly assume, moreover, that the drug is a pure substance; that is, it does not contain traces of other chemicals which might obscure, or interfere with, the results. If impurities are suspected, whole sets of separate experiments would have to be made.

Third, and most importantly, no account was taken of the possibility that your patient might have become well, or have died, in any case, even without your injecting the drug. What is needed here is experimental control; for every group of patients injected with drug solution, a precisely equal group must be injected with plain solution, without the drug. Then, by comparing results in the control and the experimental groups, one can determine whether or not the recovery or death of patients is really attributable to the drug.

Note that every experiment requires at least two parallel tests or sets of tests, identical in all respects except one. Of these parallel tests, one is the control series, and it provides a standard of reference for assessing the results of the experimental series. In drug experiments on people, not fewer than about 100,000 to 200,000 test cases, half of them controls, half of them experimentals, would be considered adequate. It should be easy to see why a single test on a single test case may give completely erroneous conclusions. Many repetitions of the same test, under as nearly identical conditions as possible, and at least one control test for each of the experi-

mental tests—these are always prerequisite for any good experiment.

While an actual drug-testing program would be laborious, expensive, and time-consuming, the design of the experiment is nevertheless extremely simple. There are few steps to be gone through, and it is fairly clear what these steps must be. But there are many experiments where the tests themselves may not take more than an hour or two, while several years may have to be spent to think up appropriate, foolproof plans for these tests.

And despite a most ingenious design and a most careful execution, the result may still not be a clear yes or no. In a drug-testing experiment, for example, it is virtually certain that not 100 per cent of the experimental, drug-injected group will recover nor 100 per cent of the untreated control group will remain sick.

The actual results might be something like 70 per cent recovery in the experimentals and something like 20 per cent recovery in the controls. The experimentals here show that 30 per cent of the patients with that particular disease do not recover despite treatment, and the controls show that 20 per cent of the patients get well even without treatment. Moreover, if 70 out of every 100 experimental patients recover, then 20 out of these 70 were not actually helped by the drug, since, from the control data, they would have recovered even without treatment. Hence the drug is effective in only 70 per cent minus 20 per cent, or 50 per cent of the cases.

Medically, this may be a major accomplishment, for having the drug is obviously better than not having it. But scientifically, one is confronted with an equivocal "maybe" result. It will probably lead on to new research, based on the new observation that some people respond to the drug and some do not, and to the new problem of why and what can be done about it.

The result of any experiment represents evidence; that is, the original guess in answer to a problem is confirmed as correct or is invalidated. If invalidated, a new hypothesis, with new experi-

ments, must be thought up. This is repeated until a hypothesis may be hit upon which can be supported with confirmatory experimental evidence.

As with legal evidence, scientific evidence can be strong and convincing, or merely suggestive, or poor. In any case, nothing has been "proved." Depending on the strength of the evidence, one merely has a basis for regarding the original hypothesis with a certain degree of confidence.

Our new drug, for example, may be just what we claim it to be when we use it in this country. In another part of the world it might not work at all or it might work better. All we can confidently say is that our evidence is based on so and so many experiments with American patients, American bacteria, and American drugs and that under specified hospital conditions and with proper allowance for unspotted errors, the drug has an effectiveness of 50 per cent. Experimental results are never better or broader than the experiments themselves.

This is where many who have been properly scientific up to this point become unscientific. Their claims exceed the evidence; they mistake their partial answer for the whole answer; they contend they have proof for a fact, while all they actually have is some evidence for a hypothesis. There is always room for more and better evidence, or for new contradictory evidence, or indeed for better hypotheses.

Theory

Experimental evidence is the basis for the fifth and final step in the scientific method, the formulation of a *theory*.

When a hypothesis has been supported by really convincing evidence, best obtained in many different laboratories and by many independent researchers, and when the total accumulated evidence is unquestionably reliable within carefully specified limits, then a theory may be proposed.

In our drug example, after substantial corroborating evidence has also been obtained from many other test localities, an acceptable theory would be the statement that "In such a bacterial disease, drug X is effective in 50 per cent of the cases."

This statement is considerably broader than the experiments on which it is based. Theories always are. The statement implies, for example, that drug X, regardless of who manufactures it, will be 50 per cent effective anywhere in the world, under any conditions, and can be used also for animals other than man.

Direct evidence for these extended implications does not exist. But inasmuch as drug X is already known to work within certain limits, the theory expresses the belief, the *probability*, that it may also work within certain wider limits.

To that extent every good theory has *predictive* value. It prophesies certain results. In contrast to nonscientific prophecies, scientific ones always have a substantial body of evidence to back them up. Moreover, the scientific prophecy does not say that something will certainly happen, but only that something is *likely* to happen, with a stated degree of probability.

A few theories have proved to be so universally valid and to have such a high degree of probability that they are spoken of as *natural laws*. For example, no exception has ever been found to the observation that if an apple is disconnected from a tree and is not otherwise supported, it will fall to the ground. A law of gravitation is based on such observations.

Yet even laws do not pronounce certainties. For all practical purposes, it may well be irrational to assume that some day an apple will rise from a tree, yet there simply is no evidence that can absolutely guarantee the future. Evidence can be used only to estimate probabilities.

Most theories actually have rather brief life spans. For example, if, in chickens, our drug *X* should be found to perform not with 50 per cent but with 80 per cent efficiency, then our original theory becomes untenable and obsolete. And the exception to the theory becomes a new observation, beginning a new cycle of scientific procedure.

Thus new research might show that chickens contain a natural booster substance in blood which materially bolsters the action of the drug. This

might lead to isolation, identification, and mass production of the booster substance, hence to worldwide improvement in curing the bacterial disease. And we would also have a new theory of drug action, based on the new evidence.

Thus science is never finished. One theory predicts, holds up well for a time, exceptions are found, and a new, more inclusive theory takes over—for a while. We may note in passing that old theories do not become incorrect but merely obsolete. Development of a new airplane does not mean that earlier planes can no longer fly. New theories, like new airplanes, merely range farther and serve more efficiently than earlier ones, but the latter still serve for their original purposes. Science is steady progression, not sudden revolution.

Clearly, knowledge of the scientific method does not by itself make a good scientist, any more than knowledge of English grammar alone makes a Shakespeare. At the same time, the demands of the scientific method should make it evident that scientists cannot be the cold, inhuman precision machines they are so often, and so erroneously, pictured to be. Scientists are essentially artists, and they require a sensitivity of eye and of mind as great as that of any master painter and an imagination and keen inventiveness as powerful as that of any master poet.

THE LIMITATIONS OF SCIENCE

Observing, problem posing, hypothesizing, experimenting, and theorizing—this sequence of procedural steps is both the beginning and the end of science. To determine what science means in wider contexts, we must examine what scientific method implies and, especially, what it does not imply.

The scientific domain

First, scientific method defines the domain of science: anything to which the scientific method can be applied, now or in the future, is or will be science; anything to which the method cannot be applied is not science.

This helps to clarify many a controversial issue.

For example, does science have something to say about the concept of God? To determine this, we must find out if we can apply the scientific method.

Inasmuch as the whole universe and everything in it may be argued to be God's work, one may also argue that He is observable. It is possible, furthermore, to pose any number of problems, such as "Does He exist, is the universe indeed His doing, and is He present everywhere and in everything?" One can also hypothesize; some might say "Yes," some might say "No."

Can we design an experiment about God? To be reliable, we would need experimental control, that is, two otherwise identical situations, one with God and one without. Now, what we wish to test is the hypothesis that God exists and is universal, i.e., that He is everywhere. Being a hypothesis thus far, this could be right or wrong.

If right, He would exist and exist everywhere; hence He would be present in *every* test we could possibly make. Thus we would never be able to devise a situation in which God is not present. But we need such a situation in order to have a controlled experiment.

But if the hypothesis is wrong, He would not exist, hence would be absent from *every* test we could possibly make. Therefore we could never devise a situation in which God *is* present. Yet we would need such a situation for a controlled experiment.

Right or wrong, our hypothesis is untestable either way, since we cannot run a controlled experiment. Hence we cannot apply the scientific method. The point is that the concept of God is outside the domain of science, and science cannot legitimately say anything about Him. He cannot be tested by science, because its method is inapplicable.

It should be carefully noted that this is a far cry from saying "Science disproves God," or "Scientists must be godless, their method demands it." Nothing of the sort. Science specifically leaves anyone perfectly free to believe in any god whatsoever or in none. Many first-rate scientists are priests; many others are agnostics.

Science commits you to nothing more, and to nothing less, than adherence to scientific method.

Such adherence, it may be noted, is a matter of faith, just as belief in God or confidence in the telephone directory is a matter of faith. Whatever other faiths they may or may not hold, all scientists certainly have strong faith in the scientific method. So do laymen who feel that having electric lights and not having bubonic plague are good things.

The scientific aim

A second consequence of the scientific method is that it defines the aim and purpose of science: the objective of science is to make and to use theories.

Many would say that the objective of science is to discover truth, to find out facts. We must be very careful here about the meaning of words. "Truth" is popularly used in two senses. It may indicate a temporary correctness, as in saying, "It is true that my hair is brown." Or it may indicate an absolute, eternal correctness, as in saying, "In plane geometry, the sum of the angles in a triangle is 180°."

From the earlier discussion on the nature of scientific method, it should be clear that science cannot deal with truth of the absolute variety. Something absolute is finished, known completely, once and for all. But science is never finished. Its method is unable to determine the absolute. Besides, once something is already known absolutely, there is no further requirement for science, since nothing further needs to be found out. Science can only adduce evidence for temporary truths, and another term for "temporary truth" is "theory." Because the word "truth," if not laboriously qualified, is ambiguous, scientists try not to use it at all.

The words "fact" and "proof" have a similar drawback. Both may indicate either something absolute or something temporary. If absolute, they are not science; if temporary, we have the less ambiguous word "evidence." Thus science is content to find evidence for theories, and it leaves truths, proofs, and facts to others.

Speaking of words, "theorizing" is often popu-

larly taken to mean "just talk and speculation." Consider, however, how successfully theorizing builds bridges!

Science and values

A third important implication of the scientific method is that it does not make value judgments or moral decisions.

It is the user of scientific results who may place valuations on them. But the results by themselves do not carry built-in values. And nowhere in the scientific method is there a value-revealing step.

The consequences of this are vast. For example, the science which produced the atomic bomb and penicillin cannot, of itself, tell whether these products are good things or bad things. Every man must determine this for himself as best he can. The scientist who discusses the moral aspects of nuclear weapons can make weightier statements than a layman only in so far as he may know more about what damage such weapons may or may not do. This will certainly influence his opinions. But whatever opinion he gives, it will be a purely personal evaluation made as a citizen, and any other scientist-or layman-who is equally well informed about the capacities of the weapons may conceivably disagree completely. Human values are involved here: science is not.

In all other types of evaluations as well, science is silent and noncommittal. Beauty, love, evil, happiness, all these are human values which science cannot peg. To be sure, love, for example, might well be a subject of scientific research, and it might show much about what love is and how it works. But such research could never discover that love is wonderful, an evaluation clear to anyone who has done a certain amount of nonscientific research.

It also follows that it would be folly to strive for a strictly "scientific" way of life or to expect strictly "scientific" government. Certainly the role of science might profitably be enlarged in areas of personal and public life where science can make a legitimate contribution. But a completely scientific civilization, adhering strictly to the rules of the scientific method, could never tell, for example, whether it is right or wrong to commit murder, or whether it is good or bad to love one's neighbor. Science cannot and does not give such answers. This does not imply that science does away with morals. It merely implies that science cannot determine whether or not one ought to have moral standards, or what particular set of moral standards one ought to live by.

Science and purposes

A fourth implication of the scientific method is that it cannot reveal purposes.

No step in the method can yield such revelations. Just as the things science discovers do not have built-in values, so they also do not have built-in purposes. To be sure, scientific results may be employed toward various purposes, but this is a different matter.

Does the universe exist for a purpose? Does man live for a purpose? You cannot hope for an answer from science, for science is not designed to tackle such questions. Moreover, if you already hold certain beliefs in these areas, you cannot expect science either to prove or to disprove them for you.

Many arguments have been attempted to show purpose from science. For example, it has been maintained by some that the whole purpose of the evolution of living things was to produce man. Here the evidence supporting the theory of evolution is invoked to prove that man was the predetermined goal from the very beginning.

This implies several things besides the conceit that man is the finest product of creation. It implies, for example, that nothing could ever come after man, for he is supposed to be the last word in living magnificence. As a matter of record, man is sorely plagued by an army of parasites which cannot live anywhere except inside people. And it is clear that you cannot have a man-requiring parasite before you have a man.

Many human parasites did evolve after man.

Thus the purpose argument at best would show that the whole purpose of evolution was to produce those living organisms which cause influenza, diphtheria, gonnorrhea, and syphilis. This even the most ardent purpose arguer would probably not care to maintain.

Those who claim to see the goal of evolution in man do not know their biology in other ways. The available evidence does not seem to support the notion of goal-directed evolutionary trends. If any pattern is discernible, it appears to be that of chance, of opportunistic seeping into all possible livelihood niches offered by the environment, of extinction here and flourishing there, depending on what random heredity and changing environmental conditions allow.

Moreover, orchids, houseflies, and hundreds of other living types are just as recent products of evolution as man. One could therefore claim just as well, and just as untenably, that the purpose of evolution was to produce orchids or houseflies, man merely being a convenient backdrop.

The essential point is that any purpose-implying argument, in this or in any other issue, stands on quicksand the moment science is invoked as a witness. For to say such and such is the goal, the ultimate purpose, is to state a human value. And we already know where science stands in this respect.

If one is so inclined, he is of course perfectly free to believe than man is the pinnacle of it all. Then the rest of the universe with its billions of suns, including the living worlds which probably circle some of them, presumably are merely immense and fancy scenery for the microscopic stage on which man struts about. One may believe this, to be sure, but one cannot maintain that such beliefs are justified by evidence from science.

This, then, is the voice of science: a voice without truths, without values, without purposes.

And it is precisely because science is unfettered by such concepts that it advances. After centuries of earnest deliberation mankind still does not agree on what truth is, values still change with the times and with places, and purposes remain as unfathomed as ever. On such shifting sands it has proved difficult to build a knowledge of nature. What little of nature we really know, and are likely to know in the foreseeable future, stands on the bedrock of science and its powerful tool, the scientific method.

THE LANGUAGE OF SCIENCE

Science as a whole

Fundamentally, science is a language, a system of communication. Religion, art, politics, English, and French are among other such languages. Like them, science enables man to travel into new countries of the mind and to understand, and be understood in, such countries. Like other languages, science too has its grammar—the scientific method; its authors and its literature—the scientists and their written work; and its various dialects of forms of expression—physics, chemistry, biology, etc.

Indeed, science is one of the few truly universal languages, understood all over the globe. Art, religion, and politics are also universal. But each of these languages has several forms, so that Baptists and Hindus, for example, have little in common either religiously, artistically, or politically. Science, however, has the same single form everywhere, and Baptists and Hindus do speak the same scientific language.

It should be clear that no one language is "truer" or "righter" than any other. There are only different languages, each serving its function in its own domain. Many an idea is an idiom of a specific language and is best expressed in that language. For example, the German Kindergarten has been imported as is into English, and the American "baseball" has gone into the world without change. Likewise, one cannot discuss morality in the language of science, or thermodynamics in the language of politics; to the extent that each system of communication has specific idioms, there is no overlap or interchangeability among the systems.

On the other hand, many ideas can be expressed

equally well in several languages. The English "water," the Latin "aqua," and the scientific "H2O" are entirely equivalent, and no one of these is truer or righter than the others. They are merely different. Similarly, in one language man was created by God; in another, man is a result of chance reactions among chemicals and of evolution. Again, neither the scientific nor the religious interpretation is the truer. If the theologian argues that everything was made by God, including scientists who think man is the result of chance chemical reactions, then the scientist will argue back that chance chemical reactions created men with brains, including those theological brains which can conceive of a God who made everything. The impasse is permanent, and within their own systems of communication the scientist and the theologian are equally right. Many, of course, assume without warrant that it is the compelling duty of science to prove or disprove religious matters, and of religion, to prove or to disprove scientific matters.

The point is that there is no single "correct" formulation of any idea which spans various languages. There are only different formulations, and in given circumstances, one or the other may be more useful, more satisfying, or more effective. Clearly, he who is adept in more than one language will be able to travel that much more widely and will be able to feel at ease in the company of more than one set of ideas.

We are, it appears, forever committed to multiple standards according to the different systems of communication we use. But we have been in such a state all along, in many different ways. Thus the color red means one thing politically, something else in a fall landscape, and is judged by a third standard in the fashion world. Or consider the different worth of the same dime to a child, to you, and to the United States Treasury. To be multilingual in his interpretation of the world has been the unique heritage of man from the beginning. Different proportions of the various languages may be mixed into the outlook of different individuals, but science, religion, art, politics, spoken lan-

guage, all these and many more besides are always needed to make a full life.

Biology

Within the language of science, biology is an important dialect, permitting travel in the domain of living things. Man probably was a biologist before he was anything else. His own body in health and disease; the phenomena of birth, growth, and death; and the plants and other animals which gave him food, shelter, and clothing undoubtedly were matters of serious concern to even the first of his kind. The motives were sheer necessity and the requirements of survival. These same motives still prompt the same biological studies today; agriculture, medicine, and fields allied to them are the most important branches of modern applied biology. In addition, biology today is strongly experimental, and pure research is done extensively all over the world. Some of this research promotes biological technology; all of it increases our understanding of how living things are constructed and how they operate.

Over the decades, the frontiers of biological investigations have been pushed into smaller and smaller realms. Some 100 to 150 years ago, when modern biology began, the chief interest was the whole plant or the whole animal, how it lived, where it could be found, and how it was related to other

whole living things. Such studies have been carried on ever since, but in addition, techniques gradually became available for the investigation of progressively smaller parts of the whole, their structures, their functions, and their relationships to one another. Thus it happened that during the past few decades, the frontiers of biology were pushed down to the chemical level. And while research with larger biological units continues as before, the newest biology attempts to interpret living operations in terms of the chemicals which compose living creatures.

Biology here merges with chemistry. Today there are already many signs that the next frontier will be the atoms which in their turn compose the chemicals, and biology tomorrow will undoubtedly merge with atomic physics. Such a trend is quite natural. For ultimately, living things are atomic things. Penultimately, they are chemical things, and only on a large scale are they plants and animals. In the last analysis, therefore, biology must attempt to show how atoms, and chemicals made out of atoms, are put together to form, on the one hand, something like a rock or a piece of metal and, on the other, something like a flower or a human baby.

This book is an outline of how successful the attempt has been thus far.

REVIEW QUESTIONS

- 1. What are the aims and the limitations of science? Review fully. In what sense is science a language, and how does it differ from other similar languages?
- 2. What characterizes the different present-day forms of science and the different specializations of scientists?
- 3. Review the steps of the scientific method, and discuss the nature of each of these steps. Define "controlled experiment."
- 4. How would you show by controlled experiment: (a) Whether or not temperature affects the rate of growth of living things? (b) Whether or not houseflies can perceive differently colored objects? (c) Whether or not plants use up some of the soil they grow in?
- 5. Suppose that it were found in Question 4a that, at an environmental temperature of 28°C, the growth of fertilized frog eggs into tadpoles occurs roughly twice as fast as at 18°C. What kinds of theories could such evidence suggest?
- 6. What are the historical and the modern relations of science and religion? Which of the ideas you have previously held about science should you now, after studying this chapter, regard as popular misconceptions?
- 7. Can you think of observations or problems which so far have not been investigated scientifically? Try to determine in each case whether or not such investigation is inherently possible.

14 THE NATURE OF SCIENCE

8. Why is mathematics not considered to be a science?

9. Consider the legal phrases "Do you swear to tell the truth and nothing but the truth?" and "Is it not a fact that on the night of...?" If phrases of this sort were to be used in a strictly scientific context, how should they properly be formulated?

10. Biology is called one of the natural sciences, all of

which deal with the composition, properties, and behavior of matter in the universe. Which other sciences are customarily regarded as belonging to this category, and what distinguishes these from one another and from biology? What are *social sciences?* Do these too operate by the scientific method?

SUGGESTED COLLATERAL READINGS

- Beveridge, W. I. B.: "The Art of Scientific Investigation," Norton, 1957.
- Conant, J. B.: "On Understanding Science," Yale University Press, 1947.
- ——: "Science and Common Sense," Yale University Press, 1951.
- ----: "Modern Science and Modern Man," Columbia University Press, 1952.

Part One

THE LIVING WORLD

A good plan of procedure in a study of living things is to begin with a characterization of the broad domain with which biology deals, namely, the whole living world in time and in space.

Just what is life? How was it created originally in the far distant past? And how did such first life become the living world of today? Questions like these are clearly fundamental, and a discussion of the origin of life undoubtedly should be part of any broad characterization of the living world.

Within this world, the outstanding object and basic unit is the individual living creature, the **organism**. What is an organism? What is it made of, and what are its properties? And what exactly distinguishes it from an inanimate object? A general characterization of the living world certainly must deal fully with these issues.

Numbers of organisms are grouped together into local **communities**. A human observer especially is likely to be aware of the communal, strikingly social organization of his own kind. And if he looks farther afield, the regional groupings of plant and other animal populations are bound to attract his attention too. An examination of the living community evidently should be included in a broad characterization of life.

Finally, even the most casual observer of the living world cannot fail to notice its most general characteristic, namely, that it exists within a larger **environment** and that this environment influences it greatly. Clearly, a discussion of the environment and of its role in life should be part of any broad characterization.

The following four chapters are devoted to these topics. We begin at the beginning, with the origin of life.

CHAPTER 2

The origin of life

As noted in the previous chapter, one of the most fruitful and significant advances in biology during the last century has been the firm recognition that all living creatures consist entirely of chemicals. Moreover, it is now also clear that before there were living creatures on earth, there were only chemicals; living things originated out of chemicals. Chemicals in turn are composed of atoms. Thus the story of the origin of life is a story of how atoms first came to be combined into chemicals, and how these then came to be arranged into "living" wholes. It should be clear that by tracing this origin, we gain important glimpses into the very nature of life.

The understanding so obtained may then serve us as a background for the later discussion of all living processes.

To be sure, our understanding of the origin of life is at present far from complete. Much of what is known about it is simply a backward projection of living types and living activities encountered today. For example, biologists deduce from viruses, bacteria, and other primitive existing forms what the earliest living forms might have been like. Other clues come from astronomy, physics, and geology, sciences which contribute information about the probable physical character of the ancient earth.

Important data are also provided by ingenious chemical experiments, designed to duplicate in the laboratory some of the steps which many millennia ago may have led to the beginning of life.

All this, supplemented to no small degree by speculation, today enables us to give a preliminary but plausible account of living origins. This account contains just enough detail to suggest how life *could* have arisen from nonlife. And it contains more than enough detail to show what we mean by the term "living."

Since, as noted above, the story of life and its origin is largely a story of chemicals, it should not be surprising that chemistry today is one of the important background sciences to biology. Indeed, much of modern biology simply is chemistry, and very many professional biologists are good chemists. You too will have to understand certain fundamentals of chemistry before you can hope to understand certain fundamentals of biology. We shall describe the necessary chemical fundamentals in the following section. In the section after that we shall then see how this knowledge helps toward understanding the origin of life.

THE CHEMICAL BACKGROUND

Atoms and molecules

The universe is made up of 92 different basic kinds of materials, called chemical elements. Iron, silver, gold, copper, and aluminum are some familiar examples of elements. Some others are listed in Table 1. Each element is made up of unimaginably tiny particles called atoms. An atom may be said to be the very smallest complete unit of an element. For example, a gold atom is the basic unit of the element gold. (You may perhaps know that every atom in turn is made up of even tinier particles, such as electrons, protons, and neutrons. This is another story and need not concern us here.)

The atoms of different elements differ in mass, or "weight." Hydrogen atoms have the least mass and are the lightest; uranium atoms have the most mass and are the heaviest. Note that in this atomic

TABLE 1. Some common chemical elements

Element	Symbol	Number of possible bonds
Hydrogen	Н	1
Sodium	Na	1
Potassium	K	1
Chlorine	Cl	1
Iodine	I	1
Calcium	Ca	2
Magnesium	Mg	2
Sulfur	S	2
Oxygen	O	2
Copper	Cu	1, 2
Iron	Fe	2, 3
Carbon	C	2, 4
Silicon	Si	4
Aluminum	Al	3
Nitrogen	N	3, 5
Phosphorus	P	3, 5

age man has learned to create artificially a number of elements still heavier than uranium. Plutonium is an example of these man-made heavy elements.

Each element is given a chemical symbol, often the first or the first two letters of its English or Latin name. Thus the symbol for hydrogen is H, that for carbon is C, that for silicon is Si. Consult Table 1 for others. To represent one atom of an element, one simply writes the appropriate symbol. For example, the letter H stands for one atom of hydrogen.

Under given conditions of temperature, pressure, and concentration, most atoms are able to attach to, and to remain linked to, certain other atoms. Such combinations of two or more atoms are called molecules. For example, when one hydrogen atom and one chlorine atom become attached to each other, the result is a molecule, namely, a molecule of hydrogen chloride. When lots of molecules of the same kind are found together, so that the whole is large enough to be seen, we call it a compound. Thus a large quantity of hydrogen chloride molecules represents the compound hydrogen chloride. We may say, therefore, that a molecule is the very smallest complete unit of a compound. Note that the relation between molecule and compound is essentially the same as that between atom and element.

To make two or more atoms link together into a molecule, work must be done; that is, an external force, or better, an external source of energy, must provide the "cement" which will hold the atoms together. Put another way, to form a bond between two atoms, bond energy must be supplied from the outside. In different cases, different forms of energy may be used. For example, heat, light, electricity, X rays, and mechanical pressure are different forms of energy, and each of them may do the work necessary to combine given atoms into a given molecule. The bond energy which then holds these atoms together is said to be chemical energy.

Because of the bond energies between its atoms, every molecule holds energy "in storage." If, then, by appropriate means a bond between two atoms is broken, the atoms separate and the bond energy is released. The amount of this energy equals the amount which had to be supplied originally to link the atoms together.

Each kind of atom has a fixed, limited bonding capacity; that is, it can form only so many bonds with other atoms (Table 1). For reasons which need not be examined here, a few types of atoms cannot form any bonds. The atoms of the elements helium, neon, and argon are among these. Such elements are chemically completely inert, and their atoms cannot participate in the formation of molecules.

Atoms of hydrogen, and of a number of other elements, may form single bonds. For example, one H atom can combine with exactly one other H atom. Each here uses up its entire bonding capacity: $H + H \rightarrow H$ —H. The single bond is indicated by the short line between H's. One hydrogen atom can also combine with one atom of chlorine, which also can form only a single bond: $H + Cl \rightarrow H$ —Cl.

Two, three, four, and even five bonds can be formed by the atoms of other elements. For example, oxygen, nitrogen, and carbon can form two, three, and four bonds, respectively. We may symbolize these bonding capacities by writing.

The two bonds of an oxygen atom could hold, for example, one hydrogen atom each. The resulting molecule, water, may be written H—O—H. Or both bonds of one oxygen atom could hold a second oxygen atom: O=O. Or the four bonds of two oxygen atoms could satisfy the bonding capacity of one carbon atom: O=C=O. For practice, and using information in Table 1, show how molecules could be formed from atoms of silicon and oxygen; potassium and iodine; copper and oxygen; iron and oxygen.

An atom may combine with several different kinds of atoms. For example, in the molecule

$$\begin{matrix} H \\ | \\ Cl - C - O - H \\ | \\ H \end{matrix}$$

the four bonds of the carbon atom hold four atoms of three different elements: Cl, H, and O. Not all atomic combinations possible on paper can actually occur in nature. What is and what is not possible here is well understood, but the matter need not be discussed in the present context.

In writing a molecule, it is not necessary to show the distribution of the bonds as above. The molecule may be written in such a way that only the types and numbers of its atoms are indicated, without reference to the bonds. In this procedure, the number of like atoms is written as a subscript to the chemical symbol. For example, the hydrogen molecule H-H may be written also as H2. Water (H-O-H) may be written also as H2O. The molecule O=C=O above, depicting the structure of carbon dioxide, may be written also as CO2. If more than one molecule of a particular type is to be represented, the appropriate number is put before the molecular formula. For example, 5H2O means five water molecules. Practice this shorthand writing with the molecules you constructed above on your own.

It should be clear that molecules differ in size and mass according to the number and the types of atoms in them. One molecule composed of few light atoms will be smaller and weigh less than another molecule composed of many heavy atoms. Thus $\mathrm{H_2O}$ is larger and heavier than $\mathrm{H_2}$. Some molecules are extremely large, containing hundreds or thousands of atoms each. As we shall see, very large molecules are particularly characteristic of living systems.

The chemical properties of a molecule are determined by the *numbers*, the *types*, and the *arrangement* of atoms. Two molecules may contain the same atoms, but if these are arranged differently, the molecules will have different properties. For example,

contain identical atoms, and both molecules may be written as $\rm C_2H_5OCl.$ But since their atoms are bonded in different patterns, they are, in fact, different kinds of molecules, with different chemical properties.

Molecules and reactions

With certain exceptions unimportant in the present context, free atoms today do not exist naturally on the surface of the earth. As we shall see shortly, atoms probably were free at one time, just after the origin of the earth. Later, however, atoms which could combine with others did so. Ever since, the earth has been very largely a collection of molecules.

Molecules are not absolutely permanent structures. If two or more of them come into contact, they may react with one another, and as a result change into different kinds of molecules. Virtually all chemical events on earth, including those which have led to, and now occur within, living creatures are contact reactions among molecules.

In the most general terms, a molecular reaction changes the number and/or the types and/or the arrangements of the atoms in the molecules. Four main categories of reactions may be distinguished. First, two or more molecules may add together and form a single, larger molecule. This is a synthesis reaction. For example,

$$CO_2 + H_2O \rightarrow H_2CO_3$$

carbon water carbonic
dioxide acid

Second, one molecule may break up into two or more smaller molecules. This is a **decomposition** reaction, and it is the reverse of synthesis. For example,

$$H_2CO_3 \rightarrow CO_2 + H_2O$$

Third, one or more of the atoms of one molecule may trade places with one or more of the atoms of another molecule. This is an exchange reaction. For example,

Lastly, the numbers and types of atoms in a molecule may remain the same, but the pattern of the atoms changes. This is a rearrangement reaction. For example,

Note that in every equation illustrating a reaction, as above, the *total* numbers and types of atoms to the left of the arrow equal exactly the totals to the right of the arrow; in the reaction as a whole, atoms are neither gained nor lost. It is important to make sure that equations *balance* in this fashion whenever a reaction is written down.

A molecular reaction possible on paper can occur actually only under appropriate conditions. What these conditions must be varies for different reactions. Temperature, pressure, and the concentration of participating molecules are some of the governing factors.

Since a reaction among molecules makes, breaks, or rearranges the bonds between some of the atoms and since bonds represent chemical energy, energy changes are likely to accompany the reaction. In synthesis, for example, at least one atom of one molecule becomes linked to at least one atom of another molecule; the new link combines the reacting molecules into a single larger one. But as noted earlier, to forge a link, bond energy must be supplied from the outside. Hence a certain amount of energy must be put into a synthesis reaction if such a reaction is to occur. Symbolically,

$$A + B + \text{energy} \rightarrow A - B$$

This describes a so-called **endergonic**, or energyrequiring, reaction. The energy becomes incorporated into the new molecule A—B.

Conversely, in a decomposition, at least one existing bond is broken, and the energy of that bond is released:

$$A-B \rightarrow A + B + \text{energy}$$

This symbolizes an exergonic, or energy-yielding, reaction. Under suitable conditions, energy obtained from a decomposition may be used to make possible a synthesis. This happens frequently in the living world, as we shall see. Energy changes usually also accompany molecular exchanges and rearrangements. Thus,

$$A-B+C-D \rightarrow A-C+B-D \pm \text{energy}$$

and

$$A \rightarrow B \pm \text{energy}$$

With the foregoing as a general background, we are now ready to examine the origin of life.

CHEMICAL EVOLUTION

The early earth

Living creatures on earth are a direct product of the earth. There is now little doubt that living things owe their origin to certain physical and chemical properties of the ancient earth. Nothing supernatural seems to have been involved—only time and natural physical and chemical laws operating within the peculiarly suitable earthly environment. Given such an environment, life probably had to happen. Put another way, once the earth had originated in its ancient form, with particular chemical and physical properties, it was then virtually inevitable that life would later originate on it also. For the chemical and physical properties of the earth permitted certain chemical and physical reactions to occur, and one result of these reactions was something living. We may infer, moreover, that if other solar systems possess planets where chemical and physical conditions resemble those of the ancient earth, then life would originate on these other planets too. Indeed, it is now believed strongly that life occurs not only on this earth, but is probably widely encountered throughout the universe.

The life-producing chemical and physical properties of the early earth were a result of the way the earth, and our solar system as a whole, came into being to begin with. The best available evidence indicates that the sun and earth are both about 41/2 to 5 billion years old. Several hypotheses have been proposed to explain the process of formation. According to one now widely accepted, the whole solar system formed from a hot, rapidly rotating ball of gas. This gas was made up of free atoms. Hydrogen atoms probably were the most abundant, and other, heavier kinds were present in lesser quantities. The sun was formed when most of this atomic gas, hence most of the hydrogen, gravitated toward the center of the ball. Even today, the sun is composed largely of hydrogen atoms. A swirling belt of gas remained outside the new sun. Eddies formed in this belt, and in time it broke up into a

few smaller gas clouds. These spinning spheres of fiery matter were the early planets.

The earth thus probably started out as a glowing mass of free hydrogen and other types of atoms. These eventually became sorted out according to weight. Heavy ones, such as iron and nickel, sank toward the center of the earth, where they are still present today. Lighter atoms, such as silicon and aluminum, formed a middle shell. The very lightest, such as hydrogen, nitrogen, oxygen, and carbon, collected in the outermost layers.

At first, temperatures were probably too high for the formation of molecules. Excessive heat disrupts the bonds between atoms as fast as such bonds might form. But under the influence of the cold of cosmic space, the earth began to cool down gradually. And in time, temperatures became low enough to permit a relatively stable bonding together of atoms. Molecules then appeared in profusion, and free atoms disappeared.

With this, we reach the beginning of the chemical history of the earth, which henceforth will accompany the physical history. Conditions were apparently appropriate for a remarkable series of chemical reactions, synthesis reactions in particular. After free atoms had combined into small simple molecules, some of these subsequently combined into larger molecules. Some of these in turn later combined into still larger molecules. After several more of such rounds of chance synthesis, spread out through many millions of years, certain extremely large molecules had formed which possessed unique, "living" properties.

As far as they are known or suspected, what are the details of these life-producing reactions?

The first round

Among the lightest and most abundant materials in the surface gas of the early earth were, as noted above, atoms of hydrogen, oxygen, carbon, and nitrogen. Therefore, when temperatures became low enough to allow the formation of molecules, the atoms of these four elements must have played a conspicuous role. Of the four, the most reactive is hydrogen; that is, hydrogen combines more readily with O, N, and C than these three combine with one another. Three types of molecules therefore must have appeared in the earth's outer layers:

H atoms combined with O atoms, producing molecules of

H atoms combined with N atoms, producing molecules of

H atoms combined with C atoms, producing molecules of

Temperatures were such that these three compounds persisted as gases, and the earth henceforth had an outer *atmosphere* containing large quantities of these three.

We have indirect evidence that these events actually occurred, not only on earth, but on some of the other planets as well. For example, today on the cold, distant planet Jupiter, water, ammonia, and methane appear to be present in the form of permanently frozen solids. Apparently, the initial chemical events there were as on earth, but at that great distance from the sun, the surface of the planet probably froze before much further chemical change could occur. The modern earth, to be sure, does not have an ammonia-methane atmosphere. We shall soon see how the present "air" may have developed.

In time, as the gas ball which was the earth continued to cool, temperatures became low enough to allow some of the gases to liquefy and some of the

liquids in turn to solidify. Heavy substances near the center of the earth probably tended to liquefy and solidify first. But the pressure produced by the weight of the overlying materials generated so much heat that any tendency to solidify was counteracted. To this day the earth contains a hot liquid or semiliquid center. On the other hand, the middle shell of lighter substances did congeal, and a solid, gradually thickening crust developed. As it thickened and cooled, it wrinkled and folded and gave rise to the first mountain ranges. Overlying this crust was the outer atmospheric mantle, which at prevailing temperatures still remained gaseous.

Then the rains started. All the water on earth up to this stage was in the atmosphere, forming clouds probably hundreds of miles thick. The solidifying crust underneath at first was sufficiently hot so that any liquid water would boil away instantly. But eventually the crust became cool enough to hold water in liquid form, and then rain began falling in unceasing, centuries-long downpours. Basins and shallows filled up, and torrential rivers tore down from the mountains. The oceans formed in this way.

Dissolved in these seas were some of the atmospheric ammonia and methane, compounds which persist as gases at temperatures at which water is liquid. Also accumulating in the ocean were salts and minerals. At first there were none, but as the rivers eroded the mountainsides and dissolved them away and as violent tides battered the shores and reduced them to powder, salts and minerals came to be added to the ocean in increasing quantities. Moreover, massive submarine bursts of molten lava probably erupted frequently through the earth's crust, and they too added their substance to the mineral content of the world's waters. Thus the oceans acquired their saltiness relatively early, and to a small extent they became saltier still during subsequent ages.

The formation first of water, methane, and ammonia and second of large bodies of *liquid* water containing methane, ammonia, and many minerals in solution were the key events which made the later origin of life possible. Water was, and is now,

the most essential single component of living matter. On an average, two-thirds, and often as much as 90 per cent or more, of anything living is water, and the presence of water in bulk over three-fourths of the earth's surface is today of profound importance in the economy of living things. The fundamental role of water traces primarily to two of its properties.

First, water is virtually the best of all possible solvents. It dissolves more of more substances than practically any other liquid, and this means that it is an ideal medium for chemical reactions. Chemical processes also occur in gases and solids, but many more can occur in liquids, and much more readily. Since living processes are based on chemical processes, the abundant supply of liquid water on the early earth was a promising circumstance.

Second, water was originally the only good source of hydrogen and oxygen. Both elements have exceedingly useful properties, and the construction of a living system on a chemical basis virtually demands their availability. But as noted, free hydrogen atoms and free oxygen atoms became unavailable soon after the origin of the earth. Water molecules then came to serve as the principal suppliers. Water remains today virtually the only usable source of hydrogen and one of the important sources of oxygen.

Thus oceanic water set the stage for the formation of living matter. The actors on this stage were the various gases and minerals dissolved in water plus water itself. And the title role was played by the carbon of the gas methane.

The second round

Properties of carbon. Carbon, with a bonding capacity of 4, is a most versatile element. In the case of methane, all four bonds of carbon hold H atoms:

But any one or more of these may be exchanged rather readily with other kinds of atoms. For example, if methane is allowed to react with chlorine or chlorine-containing molecules, one, two, three, or all four of the H atoms of methane may be replaced by Cl atoms. The resulting compounds will be CH₃Cl, CH₂Cl₂, CHCl₃, and CCl₄, of which the third is the most familiar: CHCl₃ is *chloroform*, an anesthetic. The H atoms of methane may also be replaced by many elements other than chlorine and by several different ones at the same time.

Therefore, in the oceans of the early earth, methane must have reacted with numerous other simple compounds present there and a large variety of carbon-containing molecules must have come into existence. Among the important compounds which reacted with methane undoubtedly was methane itself, as well as other carbon-containing molecules formed from methane. This points up the most interesting property of carbon: many carbon atoms may link directly to one another, in an almost infinite variety of patterns. Thus if we start with methane, one of its H atoms may be replaced by a carbon atom derived, for example, from another methane molecule:

The free bonds of the added carbon may be filled by more H atoms or by other atoms, including more carbon atoms:

Molecules containing long *chains* of carbon can be formed in this way:

$$-\overset{\cdot}{c}-\overset{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c}-\overset{\cdot}{c$$

Moreover, the carbon at one end of such a chain may combine with the carbon at the other end, and carbon rings will be produced. Benzene is a good example of this:

Many additional combining possibilities exist. For example, carbon chains can be branched, rings and chains can become joined to one another, and any of these "patterns in carbon" can extend into three as well as two dimensions. Such carbon structures form molecular "skeletons," as it were, and the free bonds of the skeletons can be fleshed out with other atoms—hydrogen, oxygen, or nitrogen, for example, which might be obtained from water or ammonia.

Note that no other kinds of atoms even approach this combining versatility displayed by carbon atoms. Clearly, carbon-to-carbon combinations introduce the possibility of tremendous *complexity*, as well as *variety*, into molecular structure. In fact, carbon-containing substances display more complexity and more variety than all other chemicals put together. Note also that two molecules with even slightly differently arranged carbon skeletons are different kinds of molecules and possess different chemical properties.

Compounds of carbon. In short, methane in the early seas probably reacted with other methane molecules, with water, with ammonia, and with many of the other types of molecules present, and the result was the appearance of new kinds of molecules containing several, often many, linked carbons. This event was a critical step in the early history of living matter. For the molecules with linked carbons eventually became the stuff out of which much of living matter was constructed. Today, carbon-to-

FIG. 2.1. The chemical structure of various types of molecules found in living systems today, which probably played conspicuous roles during the original formation of living systems.

carbon combinations occur almost exclusively within living matter, or in materials derived from living and once living matter. Because of this, such complex carbon chemicals are called organic compounds. This contrasts with water, mineral substances, metallic materials, and other inorganic compounds, which do not contain linked carbons. Inorganic substances make up the nonliving world, but very many are also found in the living world.

What were some of the first organic compounds? Among the many kinds which undoubtedly formed in the early seas, six particular groups came to have special significance in later events. These six groups are (1) the sugars, (2) glycerin, (3) the fatty acids, (4) the amino acids, (5) the pyrimidines, and (6) the

purines. Representations of the chemical structures of these six are given in Fig. 2.1. Note that in each case a carbon skeleton—either a chain or a ring—is the basis of the molecule and that various groupings of hydrogen, oxygen, and nitrogen make up the remainder.

The *sugars* are molecules consisting of H, O, and a chain of a few carbon atoms. Sugars which have six carbon atoms are extremely widespread in living matter. Of these " C_6 " sugars, *glucose* is an important example. Count the atoms in the structural formula for glucose in Fig. 2.1, and verify that the atomic formula is $C_6H_{12}O_6$. Sugars as a group belong to a larger class of organic compounds known as *carbohydrates*.

Glycerin, like the carbohydrates, consists of H, O, and C atoms. There are always three carbons in a chain, and the atomic formula may be verified as C₃H₈O₃.

The fatty acids, likewise composed entirely of H, O, and C atoms, contain carbon chains which may vary in length from 2 to 20 and more. At one end of such a chain two O atoms are present, as shown in Fig. 2.1.

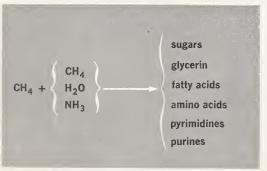
The amino acids are distinguished by the presence of nitrogen in addition to H, O, and C. In different amino acids the carbon atoms vary in number, and they may be arranged either as chains or as rings. The nitrogen always occurs in the form of an amino group, namely,

$$-\mathrm{NH}_2$$
 or $-\mathrm{NH}_2$

This group may be formed from ammonia (NH₃) by removing one H atom from it. In each amino acid, at least one amino group is joined by its free bond to the carbon skeleton of the molecule.

In the pyrimidines and the purines, the molecular

FIG. 2.2. Summary of the second round of reactions. Interaction of methane with itself, water, and ammonia probably resulted in the compounds shown on the right.



skeleton is always a ring structure, and nitrogen, in addition to carbon, forms part of the ring. As Fig. 2.1 shows, a pyrimidine molecule is built of one such ring, and purines have a double-ring skeleton.

As noted, these six groups of organic compounds were among the most important which played a role in the origin of life. We may summarize the probable manner of their formation in the early seas as in Fig. 2.2.

Since the creation of these new organic molecules occurred through synthesis reactions from simpler molecules and since chemical synthesis requires energy (see above) we may ask what the energy source might have been which would have made such reactions possible. We may ask further how we know that such reactions really took place!

Two energy sources probably made the reactions possible. One source undoubtedly was the sun. Although the dense cloud layer at first must have prevented sunlight from reaching the earth's surface (and the earth therefore must have been quite dark for long ages), the ultraviolet rays, X rays, and other high-energy radiations of the sun must have penetrated the clouds well. Some of this radiation could have provided the necessary energy for reactions among methane, ammonia, and water.

Moreover, a second energy source must have been available also: powerful electric discharges in lightning, which must have occurred almost continuously in the early cloud-laden, storm-lashed atmosphere. Like solar radiation, lightning too is capable of producing chemical reactions. Either lightning or solar energy could have acted directly on the gas molecules of the atmosphere, as still happens today to some extent. The resulting aerial chemicals could then have been washed down into the seas by rain. Alternatively, reactions could have taken place directly in the waters of the ocean, where methane and all other necessary ingredients were dissolved.

What evidence do we have that these events really happened? That they could indeed have taken place was demonstrated dramatically some years ago in laboratory experiments. Methane gas, ammonia gas,

and water were put together in a flask, and electricity was discharged into this mixture for several days to simulate the lightning discharges of the early earth. When the contents of the flask were then examined, many sugars, amino acids, fatty acids, and other simple organic compounds were found to be present!

Thus there is good reason to think that under the impact of early energy sources, simple gases and inorganic materials reacted with one another and gave rise to a variety of organic materials which accumulated in the ancient seas. These organic materials were not very complex as yet, but they contained the all-important carbon-to-carbon combinations. This was the key which was to open the door to life, for it made possible the synthesis of even larger molecules, with larger carbon skeletons and many novel chemical properties.

The third round

Once started, the joining of carbon molecule to carbon molecule continued. Among the organic substances already present, some must have reacted with one another and with inorganic materials and highly complex new types of molecules must have formed.

Specifically, sugars combined with one another. The result was a series of larger new molecules containing very long carbon chains. These new molecules, called polysaccharides, still belonged to the general category of chemicals known as carbohydrates. Some of these polysaccharides are quite familiar. For example, starch, cellulose, and glycogen are polysaccharides. Each consists of a dozen or more sugar molecules joined together. The early synthesis of polysaccharides was to prove important for the development of living systems, for, as we shall see, polysaccharides are good building materials and excellent sources of chemical energy. They still function in these capacities today.

In another series of reactions, glycerin combined with various fatty acids. Fats were formed in this manner. They too proved to be very good sources

of energy, and as building materials they came to be even more widely useful than polysaccharides.

By far the most important new construction materials formed were the proteins. These consist of amino acids joined together in exceedingly complex ways. A tremendous number of amino acid molecules—in the order of 100,000 or more—can combine to form a protein, and the geometrical pattern of such unions can vary almost infinitely. As a result, proteins are not only among the largest molecules in existence but also among the most varied structurally. Primarily because of their complexity and variety, they became the most widely adaptable building materials in the formation of living matter.

The development of proteins was important also for another crucial reason: some proteins could enormously speed up reactions among other molecules. Chemists know several methods by which a reaction of molecules may be accelerated. Application of heat, for example, is a procedure employed frequently. Many reactions can be speeded up without heating, by adding what are called catalysts. We shall see later how such materials produce this effect. Here we note only that many proteins may act as catalysts. Such protein catalysts are called enzymes. With the appearance of proteins, therefore, the chemical tempo in the early oceans could quicken substantially. And from the beginning right to the present, "living" was to become a function of enzyme-accelerated reactions.

Another group of supermolecules, at least as varied and complex as proteins, developed from the purines and pyrimidines. Some of these each combined with two other kinds of substances: sugar and phosphate. Phosphate was, and is now, one of the inorganic mineral components present in the ocean. Two types of combinations thus formed, purinesugar-phosphate and pyrimidine-sugar-phosphate. Either of these is known as a nucleotide. Hundreds and thousands of different nucleotide molecules then combined with one another, producing exceedingly complex supermolecules called nucleic acids.

We may summarize these various reactions of the third round as in Fig. 2.3.

It was the development of nucleic acids that made the ultimate formation of living matter a virtual certainty. The crucial event occurred during a fourth round of reactions.

The fourth round

As the process of progressive chemical synthesis continued, some of the polysaccharides, fats, proteins, and nucleic acids combined with one another in various ways. Among the resulting giant molecules were the nucleoproteins, combinations of nucleic acids and proteins. These are the largest and most complex molecules known. Their total complexity combines the very considerable complexities of the individual nucleic acids and proteins.

Reproduction. There are good reasons to believe that, sooner or later during their history, nucleoproteins featured several radically new properties. The most significant of these was that certain nucleoprotein molecules could make exact replicas of themselves; that is, they could reproduce!

At first glance it may seem utterly fantastic that a mere molecule should be able, by its own efforts, to make a copy of itself. But the process becomes quite plausible if we consider its details, which research is just now beginning to unravel.

FIG. 2.3. Summary of the third round of reactions. Interactions shown to the left of the arrows probably resulted in the compounds shown on the right.

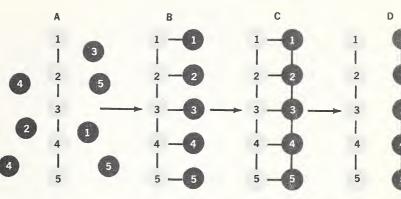
sugars + sugars	polysaccharides
fatty acids + glycerin	fats
amino acids + amino acids	proteins
purines + sugar + phosphate -	nucleotides
nucleotides + nucleotides	nucleic acids

In making an exact copy of any object, it is necessary, first, to duplicate the individual component parts of that object, and then to arrange the duplicate parts in such a way that the whole assembly will match the original. Therefore, if a copy of a nucleoprotein molecule is to be made, duplicate sugars, amino acids, phosphates, purines, and pyrimidines are required. In the early ocean, these component parts of a nucleoprotein already existed in abundance. Some of them had combined to form the original nucleoproteins, and the rest could serve later as ready-made duplicate building materials. Hence nucleoprotein reproduction became mainly a matter of arranging already existing raw materials into larger wholes which would match precisely the original nucleoproteins.

Nucleoprotein molecules are long, extended, fibrous structures. As we shall see in a later chapter, the individual sections of such a molecule have chemical affinity for like sections; that is, any segment along a nucleoprotein molecule is able to attach to itself *matching* building materials from the environment. Consequently, if all required duplicate building materials are present in the vicinity of a nucleoprotein molecule, these materials may in time become attached along the nucleoprotein in matching order. To complete the copying process, it is then necessary only to link together the "correctly" positioned duplicate parts (Fig. 2.4).

In rough outline, this is how nucleoprotein reproduction is believed to have occurred in the early seas and to occur now (see Chap. 16 for a detailed discussion). Essentially, the process represents a shortcut of the original nucleoprotein creation. Thus it would appear that the very first nucleoproteins had formed through random, manymillion-years-long sequences of reactions: by the combination of sugars, phosphates, purines, and pyrimidines into nucleotides; by the combination of nucleotides into nucleic acids; by the combination of amino acids into proteins; and by the final combination of proteins and nucleic acids. But with the appearance of the first nucleoproteins, *models* became available which could substantially accelerate

FIG. 2.4. Diagrammatic symbolization of nucleoprotein reproduction. (a) A preexisting nucleoprotein molecule (light shading) surrounded by raw materials needed for the construction of a nucleoprotein duplicate (dark shading). (b) A raw material of a given type has affinity for a corresponding component of a nucleoprotein, and the raw materials so attach in matching sequence to the preexisting nucleoprotein. (c) The correctly positioned raw materials link up with each other. (d) The new nucleoprotein molecule so created separates from the original "model." Model and replica are identical in composition.



the formation of more nucleoproteins. Each slowly created first nucleoprotein could serve as a "recipe," or a blueprint, by means of which appropriate sugars, amino acids, purines, etc., could be combined directly, in a single step and without complete dependence on chance, into exactly matching nucleoproteins.

Ever since, reproduction fundamentally has meant only this: relatively rapid construction of a duplicate of a preexisting model, out of simpler raw materials put together in a pattern matching the model. In living reproduction, the model itself carries out the matching and the putting together, and the finished duplicate may then in turn serve as a new model. In this way, descendants of the earliest nucleoproteins have followed one another in an unbroken succession down to the present.

Nucleoproteins were the first, and as far as we know, they now are the only kinds of molecules to be endowed with this capacity of *self-duplication*. This remarkable property is strictly a consequence of their particular structural make-up and atomic complexity. Put the right types and numbers of atoms together in the right way, and the whole will have the property of reproduction. In principle this is not any more mysterious, though more surprising, than that some other chemical combination of atoms should have the property of being strongly acid, for example, and thus capable of eating a hole

through steel. Reproduction, we are led to conclude, is no more and no less than one of the properties potentially inherent in matter made out of atoms. By extension, all life is no more and no less than this, as we shall see.

Nutrition. A prerequisite for reproduction was, and is now, availability of varied building materials. Therefore the multitude of inorganic and organic compounds in the early seas came to play important roles as nutrients. We may define a nutrient broadly as any kind of molecule a living system requires or may use in maintaining itself alive. And we may distinguish between organic nutrients, or foods, and inorganic nutrients. Thus the first nucleoproteins introduced not only the process of reproduction, but also that of nutrition. For reproduction was possible only with foods such as sugars, amino acids, purines, etc., and with inorganic nutrients such as phosphates and water, all present in the early seas.

As nucleoprotein reproduction transformed more and more nutrients into more and more nucleoproteins, which reproduced in their turn, everincreasing amounts of the free nutrient molecules of the seas were being used up. This probably became a serious problem. We are not sure exactly how or when it may have happened, but physical conditions on earth eventually changed in such a

way that new supplies of sugars, amino acids, and other foods could no longer be formed. Perhaps the frequency of lightning discharges decreased to such an extent that methane, ammonia, and water could no longer combine in appreciable quantities. Or perhaps because of other changes in the atmosphere, the necessary high-energy solar radiation could no longer penetrate to the earth's surface in as great an intensity as before. Quite a number of physical changes of this sort may be envisaged which would have been sufficient to stop any further synthesis of free foods. And the existing supply of such foods was being used up increasingly by the multiplying nucleoproteins.

Clearly, with the appearance of reproducing nucleoproteins, it became only a question of time when the ocean would be completely empty of free molecular foods, as empty of them as it is today. This must have meant that competition became a new condition of existence. For as they withdrew food molecules from the sea, nucleoproteins in effect began to compete for available supplies. Under such circumstances, another new property of nucleoproteins, fully as significant as that of reproduction, came to play an increasingly important role.

Evolution. As a class, nucleoproteins are exceedingly stable molecules; that is, unlike the structures of most other kinds of molecules, nucleoprotein structure is not easily disrupted by the many physical and chemical hazards encountered on earth. Occasionally, however, minor structural changes may be produced by various chemical and physical agencies. When this happens the altered nucleoprotein structure is itself very stable, and during reproduction the changed condition is transmitted faithfully into the replica. We may say that such stable changes in nucleoproteins are inheritable from one nucleoprotein generation to the next. Stable inheritable changes in nucleoproteins are known as mutations. They alter the properties of nucleoproteins in major or minor ways.

Thus, if mutations occurred in successive offspring generations, as undoubtedly happened, a single parent nucleoprotein could have given rise to a number of differently structured descendant lines. Each such mutated line would feature new and different characteristics. Some of these might, by chance, have proved to be very advantageous. For example, a mutation might have enabled a nucleoprotein to utilize as building materials previously unusable types of organic molecules. Or mutations might have allowed several nucleoprotein molecules to attach to one another and to form a united molecular aggregate. By virtue of consisting of more than one active molecule, such an aggregate might have been more effective in collecting foods than the same molecules individually. Primitive forms of cooperation may have arisen in this manner.

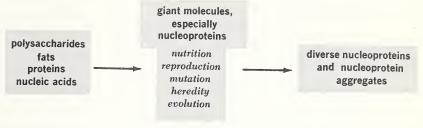
Through chance mutations of this sort, given strains of nucleoprotein molecules probably developed significant advantages over other strains in the competition for foods. The former would subsequently be able to reproduce faster and to leave more offspring molecules, whereas the latter might not even find enough foods among the slowly dwindling supplies to reproduce at all.

The final outcome would be nucleoprotein evolution. This process, to repeat briefly, would have occurred in four steps:

- 1. Origin of new nucleoprotein types by chance mutation
- 2. More effective competition, hence more abundant reproduction, of some of the new types as compared with older strains
- 3. Inheritance of the most successful new properties by an increasing fraction of the total nucleo-protein population
- 4. Eventual extinction of the least successful types Through such evolution, a succession of different and diverse nucleoproteins undoubtedly came into existence. And the elements of competition, cooperation, mutation, reproduction, inheritance, and preferential survival have governed evolution ever since (Chap. 23). We may sum up this fourth round of processes as in Fig. 2.5.

With the development of nucleoproteins, a borderline stage between life and nonlife had evidently

FIG. 2.5. Summary of the fourth round of reactions. The properties and processes which presumably characterized the earliest nucleoproteins are listed in the lower part of the second box.



been reached. Nucleoprotein molecules displayed some of the properties we now recognize as being characteristic of living matter, but truly living creatures were yet to arise.

All the events of the first four rounds of processes may be described collectively as chemical evolution: the stepwise origin and accumulation in the early seas of all the diverse molecules which eventually came to function as building materials in the construction of living matter. By contrast, the crucial events which then followed may be described as biological evolution: the actual putting together of the building materials into the first fully living units.

BIOLOGICAL EVOLUTION

The fifth round

The first truly living units, and still the basic units of all living matter today, unquestionably were cells. These are microscopic watery drops composed of a multitude of organic and inorganic molecules, including nucleoprotein aggregates in all cases. Each such drop is surrounded by a fine membrane and displays all the characteristics and properties by which we define "being alive."

If we say that biological evolution followed chemical evolution, this does not mean that chemical evolution simply stopped at one point and biological evolution then took over. On the contrary, chemical evolution continued, and indeed goes on even now. What is meant instead is that at some stage of chemical evolution an additional kind of creation took hold. Molecules no longer

gave rise just to new molecules only, but some of the molecules also produced something entirely new, something hitherto completely nonexistent, namely, fully living cells. These in turn then produced more cells, through processes of multiplication which are still going on today. Thus the new dimension of biological evolution became *superimposed* on the still continuing older dimension of chemical evolution.

The first cells. How did the first cells arise out of the varied molecular building materials in the early seas? In the whole story of the development of life, this is unquestionably the least understood chapter. We now understand quite well the general course of events up to the origin of the first cells, as outlined briefly in the foregoing, and we also understand quite well the general course of events after the origin of the first cells. But concerning that crucial origin itself we can today only speculate. Two basic kinds of hypotheses may be considered here. According to both kinds, the first cells were a more or less direct result of nucleoprotein evolution and of the progressive depletion of free foods in the early ocean.

One type of hypothesis runs somewhat as follows. As food supplies dwindled gradually, competition among nucleoproteins for available raw materials must have become increasingly intense. Among mutations which may have enhanced the competitive abilities of nucleoproteins probably were those which increased the stickiness of these molecules. Complex organic substances, proteins, for example,

tend to be sticky in any case, as everyone knows who has ever handled egg white or meat or glue. Nucleoproteins are extraordinarily sticky, and mutational changes among the first of their kind may have reinforced this property to different degrees. Thus, as indicated above, some of the early nucleoproteins may have been able to clump together into aggregates.

Such aggregates in turn may have been able to accumulate more or less extensive shells of nutrients around themselves. Carried about, such shells would represent readily available reserve foods, not easily accessible to other, competing nucleoproteins. As this device of shells became more and more successful, and necessary, several nucleoprotein aggregates might eventually have come to be embedded within a single droplike mantle of water, minerals, fats, proteins, carbohydrates, etc. In some such manner, a cell-like stage of development may have been attained.

The second kind of hypothesis differs from the above in that it assumes a different sequence of events, the end result being the same nevertheless. According to this view, nucleoprotein aggregates such as are found in primitive living cells today are considered to be far too complex to have formed purely by chance in the open ocean. It takes a preexisting living cell, with all its organized chemical machinery, to make a new nucleoprotein molecule. This is certainly true today; nucleoproteins can be constructed only within living cell-like units. Thus it is inappropriate to think that nucleoproteins came first and they then organized shell-like cells around themselves. On the contrary, cell-like units must have come first, and these subsequently constructed nucleoprotein aggregates right within themselves. The origin of the first cells therefore must be envisaged as follows. Many diverse organic and inorganic molecules in the early sea in some way condensed into tiny watery droplets, perhaps partly as a result of the sticky properties of proteins and other complex organic materials. In these condensed accumulations of molecules, many new and rapid chemical reactions were possible, because now the

molecules were very close together and could react with one another easily. A wealth of new chemical products therefore appeared, and among these were the nucleoproteins. A whole such droplet, now possessing nucleoproteins with their important new properties, in effect represented a complete cell.

With the evidence now available, we have no way of definitely choosing between these two alternative hypotheses, and indeed we must admit that the first cells might have originated in another manner altogether. But although we still do not know the actual course of origin, there can be no doubt that some course (or courses) of origin really occurred, as a fairly direct, connected consequence of the preceding chemical evolution. And with the evolution of the first cells, estimated to have taken place some two billion years ago, the border domain between the nonliving and the living had been traversed. Henceforth the earth possessed entities which were clearly alive: single-celled organisms.

Properties of early cells. What were the properties of the new cellular organisms? They not only displayed the combined properties of all the types of molecules within them, but they also featured some additional properties as a result of the close association of the varied molecules.

One of these cellular properties came to be crucial for all the others: cells were able to carry on respiration; that is, they could use some of the foods accumulated within them, or acquired by nutrition from the sea, as sources of energy. As we have seen in an earlier part of this chapter, bond energy holds together the atoms of every molecule, and every molecule is therefore a store of a certain amount of energy. By decomposing a molecule into smaller atomic groups or individual atoms, some or all of the stored chemical energy may be liberated. Organic molecules are particularly rich potential sources of bond energy, and such foods now were components of cells. In effect, therefore, decomposition reactions involving food molecules within cells could become respiration, and through it, cells could produce their own energy.

One of the byproducts of respiration was, and still is, carbon dioxide (CO2). In time, more and more respiring cells produced more and more of this gas, which passed from the cells into the ocean. Some of it dissolved there, and the remainder escaped into the atmosphere. Thus a gas not previously present in appreciable quantities began to accumulate, and we note that the physical character of the earth already was beginning to be changed by living processes. Atmospheric carbon dioxide is known to be a screen against high-energy solar radiation. The progressive accumulation of the gas in the early atmosphere therefore must have meant that certain forms of solar energy were gradually becoming unavailable on the earth's surface. As we shall see, environmental CO2 was to affect the further development of living matter in other ways as well.

The ability of early cells to produce energy within their substance made other, energy-requiring processes possible. With internal energy, all the synthesis and exchange and rearrangement reactions which previously had occurred in the open ocean could now occur inside cells. They could also occur faster and more surely, for all the reaction ingredients were aggregated closely together and proteins were directly on hand to serve as reaction-accelerating enzymes. Furthermore, since internal energy could be produced steadily, reactions within cells could become independent of chance lightning or high-energy solar radiation.

As a result, cells could synthesize not only duplicate nucleoproteins, but all their other complex organic constituents as well, out of raw materials still obtained as nutrients from the sea. These manufactured duplicate substances accumulated within cells and led to increases in cell size, or growth, and to subsequent division of a cell into two smaller offspring cells.

Moreover, with a profusion of different molecules available within cells, entirely new chemical reactions became possible, such as had not occurred previously in the ocean. New endproducts with new properties consequently could form, and during the

life of a cell, these could change cellular structure and/or behavior. In this way, cells could undergo internal development.

Also, the various cellular activities came to be harmonized and mutually adjusted in rate and amount to the requirements of the moment. As we shall see later, such control of cellular activities is achieved particularly by the nucleoproteins within cells. Through nucleoproteins, cells not only reproduce and evolve, but also maintain self-adjusting steady states despite fluctuations of environmental conditions. The nucleoproteins which serve as the ultimate directors and adjusters of cell function are called genes. We shall see in a later chapter how they carry out their multiple jobs. Here we merely note that the genes found today in all cells of all living creatures undoubtedly are descendants of the original nucleoproteins of the first cells and that, then as now, these nucleoproteins functioned not only in reproduction and evolution, but also in directing and coordinating cellular activities.

In sum, early cells were undoubtedly capable of nourishing themselves, of respiration, and of synthesis. Moreover, they could maintain steady states, grow, develop, reproduce all their internal components, including their nucleoproteins (genes), and they could divide. And by virtue of their nucleoproteins they could also mutate and evolve. Together, these various capacities established their "living" character.

Cells and viruses. The earliest cells probably possessed more than one gene-containing nucleo-protein clump each. These clumps were suspended free within the cell substance, and it must have happened frequently that one or another of the clumps broke free from the cell interior and emerged into the open ocean. In this free state, such a nucleoprotein clump would have been simply a lifeless and inert chemical aggregate, for it lacked its cellular "housing." But it must have happened often that such inert aggregates by accident met up with other early cells, and entered them. Within such new host cells the inert aggregates could be-

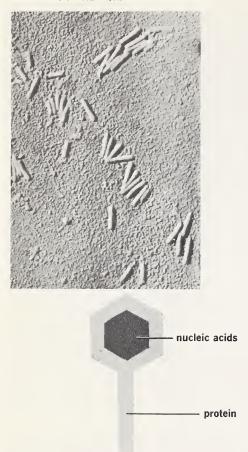


FIG. 2.6. The shape and structure of modern viruses. The photo is an electron micrograph of rod-shaped viruses. Virus types of many other shapes are known. The diagram shows the typical composition of viruses, with nucleic acid in the center and a protein shell on the outside. (Photo, R. W. G. Wyckoff, "Electron Microscopy," Interscience Publishers, Inc., 1949.)

come active again; i.e., the living machinery of the host could again provide the means for the nucleoprotein to reproduce.

Such nucleoprotein clumps, escaped from one cell, existing free for a time in an inert state, and then reentering and being reactivated by another cell, may have been the ancestors of the modern viruses. Viruses today behave exactly like this. First, they are nucleoprotein in composition; that is, they consist of a gene-containing nucleic acid core and a shell of protein surrounding this core (Fig. 2.6; note, therefore, that viruses are not "cells," but considerably less than cells). Second, we know that at least some viruses arise by breaking off from the nucleoprotein mass of a given cell, and then the so-formed viruses exist free in air or water. Further, we know that all modern viruses are quite inert in the free state and that they become reactivated if, and only if, they enter some new cell. This is an infection process, and all viruses can therefore be classified as parasites. It is quite reasonable to suppose that virus formation and virus transfer to other cells occurred as soon as cells themselves were in existence. And this is why the ancestors of modern viruses are thought to be as ancient as the very earliest cells.

An important consequence of the transfer of viruslike nucleoproteins between and among the first ells was that the transferred nucleoproteins removed given properties from some cells and added these properties to other cells. For as some of the nucleoproteins became shuffled among cells, so did the activities which these nucleoproteins controlled. This undoubtedly speeded up the process of cellular evolution, along with mutations, and contributed to the emergence of a great variety of different cell types.

Early cell types. Among the various cell types which eventually appeared, two main categories came to have particular significance in later evolution. As noted above, the earliest ancestral cells each probably possessed several gene-containing nucleoprotein clumps. In some of the descendants of these cells, the several clumps apparently aggregated together rather loosely, and the more or less condensed collection of all this nucleoprotein simply

remained embedded in the cell substance, in direct contact with it.

The group of organisms which featured such an internal cellular arrangement may be referred to collectively as the Monera. Representatives of this group are still in existence today; the most familiar of the Monera are the bacteria (Fig. 2.7). The exact ancestry of modern bacteria is somewhat in doubt. But in structure as well as function, bacteria now living are very close to our conception of what the first Monera might have been like, and the latter may conceivably have been the ancestors of modern bacteria.

Another group now living and probably descended from the first Monera are the blue-green algae. Chapter 7 will show that these primitive cellular organisms are not usually blue-green and indeed are probably not really true algae. Instead they resemble bacteria in many ways, including the way in which nucleoprotein is arranged within their cells. We may say, therefore, that the very first cells on earth probably gave rise to an early group of Monera and that these in turn were the ancestors of the modern Monera, represented today chiefly by the bacteria and the blue-green algae.

In a second major cellular type descended from the very first cells, the gene-containing nucleoprotein clumps in each cell also condensed together into a central mass. But in addition, a fine membrane formed around this mass, and the nucleoprotein thus was no longer in direct contact with the rest of the cell substance. Such a membrane-enclosed nucleoprotein aggregate within a cell is now known as a cell nucleus. Early cells which evolved a distinct gene-containing nucleus may be referred to collectively as the **Protista**. These came to be the ancestors of the vast majority of modern organisms, i.e., of all except the Monera.

The fifth round of "genesis" is summed up in Fig. 2.8. We note that this round led to the emergence of early viruses, of early moneran cell types, and of early nucleated, protistan cell types. In a subsequent round, the first plantlike and animallike organisms were to make their appearance.

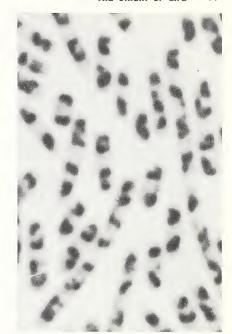


FIG. 2.7. The dispersed nucleoproteins of bacteria. The name of the bacteria shown here is Escherichia coli. Some of the cells occur as single individuals; others are joined into chains. Staining makes the nucleoproteins appear as dark bodies. Note the dispersion of these bodies throughout the cell substance of a bacterium. (Society of American Bacteriologists, from A. G. Smith, "J. Bacteriol.," vol. 59, 1950.)

The sixth round

As the free foods of the ocean were being used up more and more, the distinct prospect loomed large that the new life would soon suffer death from starvation. But through their capacity of evolution, living organisms were, and still are today, able to adapt to changing environments and to develop new, more suitable ways of life. The early organisms, in fact, did not succumb. On the contrary, they flourished and gave rise to the far-flung, richly diversified living world of today.

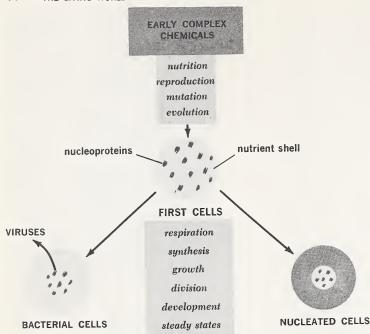


FIG. 2.8. Summary of the fifth round of reactions. Early complex chemicals with certain properties probably gave rise to the first cells, distinguished by additional properties. Such cells probably developed into two structural types, one without and one with nuclear membrane. Viruses may have formed from nucleoproteins which escaped from the cellular droplets.

Parasites, saprophytes, and eaters. One of the first evolutionary responses to dwindling food supplies probably was the development of parasitism. If foods could not be obtained from the open ocean, they still could be obtained within the bodies of living cells. As already noted, a virus, for example, could penetrate right into a cell and use the foods accumulated in such a host. Also, a small cell could solve its food-supply problem similarly if it could manage to invade a larger cell. Methods of infecting cellular hosts undoubtedly evolved early, and today all viruses, as well as many of the descendants of the first Monera and Protista, are infective and parasitic.

For many of the early organisms, parasitism undoubtedly was an effective new way of life. Another new way which required relatively little evolutionary adjustment was saprophytism. Here an organ-

ism drew food molecules, not from the decreasing supply in the ocean, but from the bodies of dead or decaying cells. Many early bacterial groups probably adopted this comparatively easy method of getting food and became the ancestors of the many modern saprophytic bacteria. Note that organic decay is a result of the nutrient-gathering activities of saprophytic bacteria. Before the development of saprophytism, decay was unknown on earth. Today, saprophytic bacteria are so abundant that virtually any substance derived from once living matter begins to decay almost immediately after exposure to air or water.

A third new way of surviving despite dwindling food supplies was to develop means of eating other living cells whole. This required the evolution of cellular mouths or equivalent engulfing structures and of devices to extract usable food molecules from

the swallowed organisms. Some of the early Protista took this evolutionary path, and they were the first animal-like cellular types.

But all three of these new food-gathering procedures were essentially self-limiting. Parasitism, saprophytism, and eating merely increased the rate of utilization of existing foods, and they did not add new food to the global supply. Clearly, if a totally new food source had not become available, life would have had to cease sooner or later.

Chemosynthesizers. What was needed fundamentally was a new way of making organic substances, preferably right within cells. The original way, in which sun and lightning made methane, ammonia, and water combine, was no longer adequate, if it occurred at all at that late period. But the raw materials for a new process were still available in abundance. Water was in inexhaustible supply, and in addition to methane, there now existed an even better source of carbon, obtainable directly within cells: carbon dioxide, byproduct of respiration. Given CO2 and water, organic molecules could be manufactured in cells, provided that a new source of energy could be found. Organic molecules themselves were good potential-energy sources, but these were the very substances which were fast disappearing and thus needed to be built in new ways.

Certain of the primitive bacterial organisms did find new external sources of energy: in sulfur, in iron, in nitrogen, and in a number of other metallic and nonmetallic materials obtainable from the environment. Several groups of the early bacteria must have evolved in such a way that they could absorb various inorganic molecules into their substance and there make them undergo chemical reactions. In some of these reactions chemical bonds were broken and energy was released. Such energy could then be used within the cells to combine CO₂ and water into food molecules. The whole process is called chemosynthesis (Fig. 2.9). Certain bacteria living today still manufacture foods in this manner (Chap. 10).

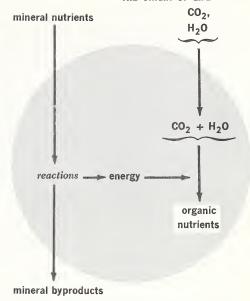


FIG. 2.9. The general pattern of chemosynthesis. With energy obtained from inorganic nutrients, the organism creates new organic nutrients out of carbon dioxide and water.

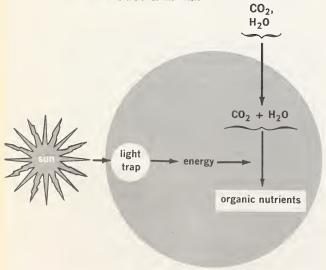
Judging from the results some two billion years later, early chemosynthesis apparently was only a limited solution of the energy- and food-supply problem. Possibly it depended too much on particular inorganic materials, available only in particular localities. A more generally useful solution required a steady, more nearly universal energy source. Such a source was the sun.

Photosynthesizers. High-energy solar radiation could no longer be had on the earth's surface in sufficient amount. But radiation of lower energy content, especially light, beamed down to earth as predictably and dependably as could be desired. If sunlight could be used, the energy problem, hence the food problem, would be solved. Indeed, sunlight became the ultimate energy supplier for

the vast majority of organisms, and it has played this role ever since.

Utilization of light energy within cells requires a cellular light-trapping device. Certain kinds of molecules are known to be able to absorb light and to trap more or less of its energy. By chance reactions, such molecules may have formed very early in the open ocean, along with all the others we have discussed. And it is likely that some of these molecules were among the many materials which collected together and formed cells. Alternatively, light-trapping molecules might have been manufactured directly within cells already in existence, as one of the new materials produced by cellular synthesis. In some such way, presumably, certain early cellular organisms came to possess molecules which were more or less efficient in trapping the energy of sunlight. Released subsequently within

FIG. 2.10. The general pattern of photosynthesis. With energy obtained from the sun and by means of energy-trapping molecules such as chlorophyll, the organism creates organic nutrients out of carbon dioxide and water.



such cells, this energy could be used to combine CO₂ and water into organic molecules.

The most efficient of the early light-trapping substances has been perpetuated to the very present. It is green, and we call it **chlorophyll**. The new process, in which sunlight and chlorophyll promote the combination of CO₂ and water into foods, is called **photosynthesis** (Fig. 2.10).

With this new source of organic molecules assured, it did not matter that free primeval foods in the ocean finally disappeared. Photosynthesizing cells could make foods for themselves, animal-like organisms could eat such cells and then each other, parasites could invade photosynthesizers or eaters, and saprophytes in turn could find foods in the dead bodies of any of these. Consequently, excepting only the chemosynthesizers, which made their own foods, all other organisms were saved from premature extinction by photosynthesis. Today photosynthesis still supports all living creatures except the chemosynthesizers.

Organisms which developed photosynthetic capacity were the first plantlike types. They arose both among the early Monera and the early Protista. Certain bacterial groups are still photosynthetic today, as are most blue-green algae. And early photosynthetic Protista were the ancestors of all true green plants now in existence.

We note that, sooner or later after the appearance of the first cells, five kinds of food-getting methods had developed: parasitism, saprophytism, eating, chemosynthesis, and photosynthesis. Only the last two added to the net global supply of foods. The Monera apparently adopted all methods except eating, and the Protista, all methods except chemosynthesis. Moreover, there is good evidence (Chap. 7) that early Protista probably possessed both animal-like eating capacity and plantlike photosynthetic capacity simultaneously. True plants then arose from this stock by loss of the animal-like eating capacity, and true animals, by loss of the plantlike photosynthetic capacity.

The evolutionary events of this sixth round may be summarized as in Fig. 2.11. In a final round, the physical earth was to acquire more or less recognizably modern features.

The seventh round

In the course of the evolution of early organisms, photosynthesis occurred to an ever-increasing extent and brought about far-reaching changes in the physical environment. As we shall see later, a byproduct of photosynthesis is free molecular oxygen (O2), a highly reactive gas which combines readily with other substances. Before the advent of photosynthesis, free oxygen had not existed since the early days of the earth, when oxygen atoms were still uncombined. Later, such small quantities of free oxygen as might occasionally have formed would have combined quickly with materials in the vicinity. Now, increasingly large amounts of free oxygen escaped from photosynthesizing cells into the ocean, and from there into the atmosphere. The gas must have reacted promptly with everything it could, and this probably initiated a slow, profound "oxygen revolution" on earth (Fig. 2.12).

Oxygen probably reacted with methane and transformed it into carbon dioxide:

$$CH_4 + 2 O_2 \rightarrow CO_2 + 2H_2O$$

Oxygen also must have reacted with ammonia and converted it into molecular nitrogen (N_2) :

$$4NH_3 + 3O_2 \rightarrow 2N_2 + 6H_2O$$

These events ultimately transformed the ancient atmosphere into the modern one, which no longer contains methane and ammonia. Instead, it consists mainly of water vapor, carbon dioxide, and molecular nitrogen, plus large quantities of free molecular oxygen itself.

At higher altitudes, under the impact of highenergy radiation from space, oxygen molecules combined with one another. The result was a layer of ozone (O₃). This layer, several miles up, has been in existence ever since. Ozone formed an even better screen than carbon dioxide against deep penetration of high-energy radiation. Consequently, organ-

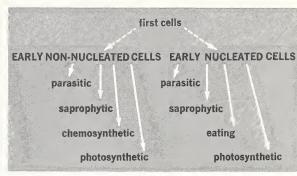


FIG. 2.11. Summary of the sixth round of reactions. This shows how the earliest living things became diversified according to the methods of food getting they evolved.

isms which evolved after the establishment of the ozone layer lived in an environment more or less completely free of high-energy radiation. This is why modern advanced plants and animals are comparatively unadapted to such radiation and are killed by even small doses of it. By contrast, the earliest organisms had evolved before the large-scale formation of ozone and had become more or less well adapted to space radiation. Their modern relatives have inherited this radiation resistance and now can withstand exposures to X rays and similar radiation that would kill an army of men.

FIG. 2.12. Summary of the seventh round of reactions, the "oxygen revolution." Oxygen resulting from photosynthesis reacted with other materials as shown and brought about the changes indicated.

$$\begin{array}{ccccc} \text{CH}_4 + 2 \text{ O}_2 & \text{CO}_2 + 2 \text{H}_2 \text{O} \\ 4 \text{NH}_3 + 3 \text{ O}_2 & 2 \text{N}_2 + 6 \text{H}_2 \text{O} \\ \text{O}_2 + 2 \text{ O}_2 & 2 \text{ O}_3 \text{, ozone} \\ \text{metals, minerals} + \text{O}_2 & \text{ores, rocks} \\ \text{organisms} + \text{O}_2 & \text{aerobic respiration} \end{array}$$

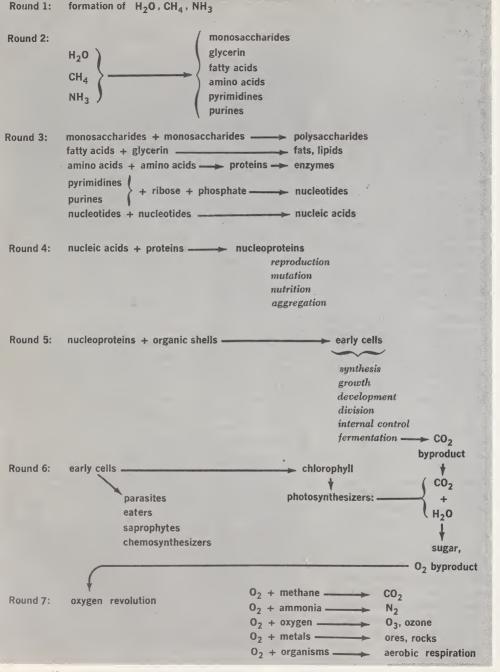


FIG. 2.13. Overall summary of the seven rounds of "genesis" described in this chapter.

Free oxygen also reacted with the solid crust of the earth and converted most pure metals and mineral substances into *oxides*, the familiar ores and rocks of which much of the land surface is now made. A few relatively unreactive metals like gold resisted the action of oxygen, but others could not. And if today we wish to obtain pure iron or aluminum, for example, we must smelt or otherwise process appropriate ores, to separate out the firmly bound oxygen.

Free oxygen, finally, made possible a new, much more efficient form of respiration. The earliest cells decomposed food molecules without oxygen, a method of energy reproduction named fermentation, or anaerobic (without air) respiration. However, if oxygen is available, it may participate in respiration. The amount of energy then obtained, per unit amount of food consumed, is much greater than in fermentation. When free environmental oxygen began to accumulate in quantity, newly evolving organisms developed means to utilize this gas. Thus an aerobic (with air) form of respiration came into existence, and it soon became the standard way of extracting energy from foods.

We note that the effects and activities of the early organisms greatly altered the physical character of the earth and also the biological character of the organisms themselves. So it has been ever since, even if never again so dramatically and incisively: the physical earth creates and influences the development of the biological, and the biological earth then reciprocates by influencing the development of the physical.

We have traced the major stages of the earth's early history, as these are understood today (Fig. 2.13). In these seven non-Biblical rounds of "genesis," no one point really qualifies as a "beginning" of life. The cell is the major product of the seven rounds, and we regard this product as being alive. But the earlier nucleoprotein already possessed some of the characteristic properties. Nucleoproteins in turn did not originate them, but acquired them piecemeal from various simpler molecules. The potential of life clearly traces back to the original individual atoms, and the creation of life out of atoms was but a step-by-step exploitation of their properties. Each of the steps spanned literally eons of chemical, and later also of biological, evolution, and any one step overlapped and integrated with the next unimaginably slowly.

Thus, unlike Athena, who sprang fully formed and armed from Zeus's head, life did not burst forth from the ocean finished and ready. Instead, life developed, and here is perhaps the most dramatic illustration that small beginnings may have surprisingly large ends. Development has been the hallmark of life ever since, and life today is still unceasingly forming and molding. Indeed, it will never be finally "finished" until its last spark is extinguished.

REVIEW QUESTIONS

1. Consider the following equation:

$$Ca(OH)_2 + 2HCl \rightarrow CaCl_2 + 2H_2O$$

- (a) Identify the different atoms by name, and determine the bonding capacity of each. (b) Rewrite the equation so as to show the atomic bonds within each molecule.
- (c) Is the equation balanced? (d) Is this an exchange, synthesis, decomposition, or rearrangement reaction?
 - 2. Review the role of (a) temperature, (b) water,

- (c) organic compounds, and (d) enzymes in the origin of life.
- 3. What is chemical energy, and what makes organic compounds particularly good sources of such energy?
- 4. What are the principal properties of nucleoproteins, and what roles have these properties probably played in the origin of life? What are genes?
- 5. What are nutrients? What factors may have contributed to their disappearance from the early ocean, and in what different ways have early organisms then ob-

tained foods? Review the general nature of each of these ways.

6. What was the physical character of the earth at the time it formed, before life originated, and after life

originated? Review the principal events of the oxygen revolution.

7. Review the whole step-by-step sequence of events by which cellular life is now believed to have originated.

SUGGESTED COLLATERAL READINGS

- Miller, S. L.: A Production of Amino Acids under Possible Primitive Earth Conditions, Science, vol. 117, 1953.
- Urey, H.: The Origin of the Earth, Sci. American, vol. 187, 1952.
- Wald, G.: The Origin of Life, Sci. American, vol. 191, 1954.

CHAPTER 3

Cell and organism

The result of genesis was the living organism. The first cells were organisms, and in the course of time they evolved into different organisms, some still unicellular like their ancestors, others multicellular. The living world today is a varied collection of unicellular and multicellular organisms.

Among these various plant and animal organisms, four main categories may be distinguished (Table 2 and Fig. 3.1). We shall have much more to say about these categories in later chapters. Here, however, our purpose is not to discuss the different characteristics of these groups, but rather their similar characteristics. What is basic and common

to *all* organisms? What does "being alive" actually mean? And how does a living organism differ from a dead one, or from a nonliving structure like a machine?

We shall deal with these questions by concentrating first on the functional features and then on the structural features of living organisms generally.

FUNCTIONAL CHARACTERISTICS

From a functional standpoint, all organisms perform the various activities which early cells had already performed. These activities may be grouped

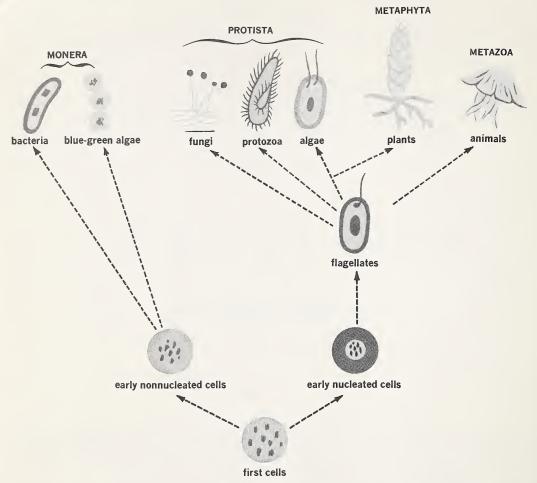


FIG. 3.1. The four main groups of presently living organisms and their probable evolutionary relationships. See also Fig. 7.2.

into two broad categories of functions, namely, metabolism and self-perpetuation.

Metabolism comprises the functions of nutrition, respiration, and synthesis and all processes associated with these three. Nutrition provides the raw

materials for life. Respiration extracts energy from some of the raw materials. With a portion of this energy, synthesis transforms the other raw materials into structural components of living matter. The remainder of the energy and all the structural

TABLE 2. The main categories of living organisms*

•			
Category	Probable ancestors	Main subgroups	
Monera	Ancient Monera	Bacteria, blue-green al- gae	
Protista	Ancient Protista	Algae, fungi, protozoa, slime molds	
Metaphyta	Ancient Protista (early algal types)	Bryophytes (moss plants), tracheophytes (vascular plants, e.g., ferns, seed plants)	
Metazoa	Ancient Protista (early algal and protozoan stocks)	Sponges, coelenterates (e.g., jellyfish), various categories of "worms," mollusks (e.g., clams, snails, squids), arthropods (e.g., insects, spiders, lobsters), echinoderms (e.g., starfish, sea urchins), vertebrates (fishes, amphibia, reptiles, birds, mammals)	

^{*} Protozoa and all Metazoa are traditionally regarded as "animals"; all other groups listed are usually designated as "plants."

components then make self-perpetuation possible (Fig. 3.2).

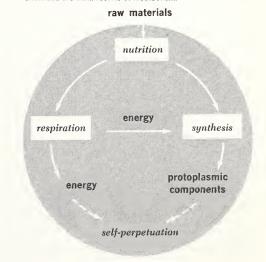
In principle, metabolism occurs also in inanimate machines. A machine may be designed to take on "nourishment," in the form of fuel and raw materials. The fuel may provide operating energy, and with it the raw materials may then be processed into nuts, bolts, shafts, and other structural components out of which such a machine is built. If, for one reason or another, any one of these processes should stop, the machine would cease to operate, even though it is still whole and intact. Similarly, if a metabolic function of an organism is stopped, the organism becomes nonoperational and dies.

Metabolism therefore may be said to run the machinery of life. But metabolism, having equivalents in inanimate nature, is not the distinguishing feature of living nature. That distinguishing feature is, rather, self-perpetuation. Self-perpetuation ensures that the machinery continues to run indefinitely, without outside help and despite internal or external changes which would otherwise stop its operation.

Based on the energy and the structural components supplied by metabolism, self-perpetuation itself includes three principal activities: steady-state control, reproduction, and adaptation (Fig 3.3.). All three allow the organism to cope with the disruptive and destructive effects of the *environment*, in far greater measure than the operations of any machine can do. And it is primarily this which puts the organism into the category of the living and the machine into that of the inanimate.

Fundamentally, steady-state controls permit the organism to receive information from within itself and from the external environment and to act on this information in a self-preserving manner. The information is received in the form of stimuli, and

FIG. 3.2. The interrelations of the main processes of metabolism and the main results of metabolism.



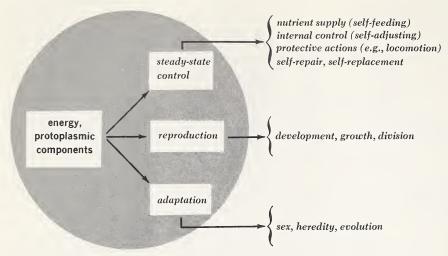


FIG. 3.3. The interrelations of the main processes of self-perpetuation and the main results of these processes.

the self-preserving actions are responses. Thus, with the aid of energy and building materials, steady-state controls cause the organism to procure fresh nutritive raw materials when past supplies are used up; adjust respiration and synthesis in rate and amount according to the requirements of the moment; channel the energy of respiration into protective physical responses like movement and into protective chemical responses like poison manufacture; and channel the products of synthesis into repairing damaged parts of the organism, into completely replacing irreparable parts, and into constructing additional parts, hence into growth.

Many machines of advanced, modern design have ingenious steady-state controls built into them too. For example, such controls may make a machine automatically self-"feeding" and self-adjusting. But no machine is as yet self-protecting, self-repairing, or self-healing to any major extent, and no machine certainly is self-growing. On the other hand, it is known today how, theoretically, such a fully self-controlled, self-preserving machine could be built.

If it is ever built, it will have steady-state controls conceivably quite as effective as the ones which have been standard equipment in living organisms for a billion years.

Steady-state controls permit an organism to live as long as it inherently can. Life span is invariably limited because, like any other parts of an organism, those which maintain steady states are themselves subject to wear and tear, to breakdown, and to accidental destruction. When some of its controls become inoperative for any such reason, the organism suffers disease. Other, still intact controls may then initiate self-repair. In time, however, so many controls break down simultaneously that too few remain intact to effect repairs. The organism then is in an irreversibly unsteady state, and it must die. In this regard, the organism again resembles a machine. For even the most carefully serviced apparatus eventually becomes scrap, and the destructive impact of the environment ultimately can never be denied.

But unlike a machine, the organism here outwits

the environment. For before it dies, the organism may have reproduced. With the help of energy and raw materials, the living organism has grown in size, and growth in size subsequently permits subdivision and growth in numbers. Reproduction in a sense anticipates and compensates for unavoidable individual death. And through reproduction over successive generations, the tradition of life may be inherited and carried on indefinitely.

Reproduction implies a still poorly understood capacity of *rejuvenation*. The material out of which the offspring is made is part of the parent, hence is really just as old as the rest of the parent. Yet the one lives and the other dies. Evidently, there is a profound distinction between "old" and "aged." Reproduction also implies the capacity of development, for the offspring is almost always not only smaller than the parent, but also less nearly complete in form and function.

In its capacity of reproduction, the organism far outclasses any inanimate system. No machine self-reproduces, self-rejuvenates, or self-develops. However, it may be noted once again that the theoretical knowledge of how to build such a machine now exists. A device of this kind would metabolize, maintain steady states, and eventually "die," but, before that, would reproduce. It would be almost living. If it had the additional capacity of adaptation, it would be fully living—and here too the theoretical know-how is already available!

Adaptation is the final requirement for circumventing destructive effects of the environment. For steady-state controls and reproduction as such cannot counteract major, long-term environmental change. Over thousands and millions of years, climates may become altered profoundly; ice ages may come and go; mountains, oceans, vast tracts of land may appear and disappear. Moreover, living organisms themselves may in time alter the nature of a locality in major ways. Consequently, two related organisms many reproductive generations apart could find themselves in greatly different environments. And whereas the steady-state controls of the ancestor may have coped effectively

with the early environment, these same controls, if inherited unchanged by the descendant, could be overpowered rapidly by the new environment. Hence, in the course of reproductive succession, organisms must change with the environment if they are to persist. They actually do change through adaptation. Evolution is the means of adaptation, and evolution in turn is made possible through mutation and also through sex and heredity, as we shall see.

To define, then, the fundamental meaning of "living," we may say that any structure which metabolizes and self-perpetuates is alive. And we find further that the metabolic functions of nutrition, respiration, and synthesis make possible the self-perpetuative functions of steady-state control, reproduction, and adaptation.

A first implication of this is that any structure which does not satisfy the above in every particular is either nonliving or is dead if it was once alive. Every nonliving or dead object on earth sooner or later decomposes and crumbles to dust under the impact of the environment. But every living object metabolizes and self-perpetuates and so may avoid such a fate. We come to realize that living matter, though soft and weak to the touch, is actually far more durable than the strongest steel, far more permanent than the hardest granite. Oceans, mountains, even whole continents have come and gone several times during the last two billion years, but living matter has persisted indestructibly during that time and, indeed, has become progressively more abundant.

A second implication of the definition above is that the property of life basically does not depend on a particular substance. Any substance, of whatever composition, will be "living" provided that it metabolizes and self-perpetuates. It happens that only one such substance is now known. It is shaped into organisms, and it is a complex mixture of many inorganic and organic compounds, as outlined in the preceding chapter. We call this type of material "living matter," or protoplasm. But if some day we should be able to build—and we almost surely shall

—a fully metabolizing and self-perpetuating system out of nuts, bolts, and wires, then it too will have to be regarded as being truly alive. Similarly, if some day we should encounter, on another planet out in space, a metabolizing and self-perpetuating entity made up of hitherto completely unknown materials, it also will have to be considered living. It may or may not be "life as we know it," that is, life based on cells, genes, proteins, fats, water, etc., but it will be truly living if it metabolizes and self-perpetuates.

A third implication is that a comprehensive study of organisms must deal with four major topics:

- 1. The changing *environment*, which created the organism, which supplies the nutritive raw materials for metabolism, and which orients the self-perpetuation of the organism
- 2. Protoplasm, the material which possesses the properties of life and out of which organisms are made
 - 3. Metabolism, which maintains living processes
- 4. Self-perpetuation, which endows organisms with potential immortality

A glance at the table of contents will show that this book is structured along these very lines.

The above characterizes organisms from the functional standpoint. What is their structural character?

STRUCTURAL CHARACTERISTICS

Levels of organization

During the process of genesis in the early seas, the keynote and central running theme were progressive aggregation. As we have seen, atoms aggregated into simple molecules; simple molecules aggregated into complex ones; complex molecules aggregated into molecular clumps; and clumps and other molecules eventually aggregated into cells.

The stages of aggregation may be regarded as successively higher levels of organization of matter. As noted, each level features new properties over and above those found at lower levels. For example,

a molecule exhibits new properties over and above those of the individual atoms. Similarly, a cell exhibits important properties in addition to those of the molecular aggregates which compose it. Such additional properties in a sense represent the dividend on the energy required to raise one level to the next higher.

The aggregative tendencies which led to higher organizational levels did not cease to operate with the formation of cells. Multicellular organisms arose in due course, and within them, a number of supracellular levels came to be established. Above the level of the cell today is the tissue, defined as an aggregation of like cells performing similar functions. Above the tissue level is the organ, a cooperative aggregation of several different tissues. And above the organ level is the organ system, a cooperative aggregation of several different organs. Several organ systems make up modern multicellular organisms.

Aggregation has carried also beyond the organism. A few individual organisms of one kind together may make up a family. Large numbers of families of one kind may make up a society. All organisms, families, and societies of the same kind together form a species. Different species aggregate into a local community. And the sum of all local communities represents the whole living world (Fig. 3.4).

Each of these living levels features properties beyond those of lower ones. Also, each of these levels is structurally more complex than lower ones, for it combines the complexities of all lower levels and has an additional complexity of its own. Moreover, each level includes fewer members than the preceding. Thus there is only one living world, but there are uncountable numbers of atoms. We note, in sum, that from atom to living world, matter is organized into a *hierarchy* of structural levels.

From this, we arrive at *structural* characterization of life, nonlife, and death. Up to the level of the molecular aggregate, matter is nonliving. At all higher levels matter is living, provided that, at *each* such level, metabolic and self-perpetuative functions

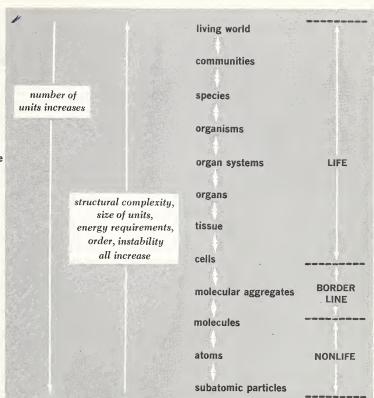


FIG. 3.4. The hierarchy of levels in the organization of matter.

are carried out. To be living, a society, for example, must metabolize and self-perpetuate on its own level, as well as on every subordinate level, down to the molecular aggregate.

As life is organized by levels, so is death. Structural death occurs when one level is disrupted or decomposed into the next lower. For example, if a tissue is disaggregated into separate cells, the tissue ceases to exist. But note that disruption of one level need not necessarily mean disruption of lower levels. For if a tissue is decomposed into cells, the cells may carry on individually; if a family is dis-

rupted, the member organisms may survive on their own. On the other hand, death of one level does always entail death of higher levels. If many or all of its tissues are destroyed, the whole organ will be destroyed; if many or all of its families are dismembered, a society may cease to exist. In general, the situation is comparable to a pyramid of cards. Removal of a top card need not affect the rest of the pyramid, but removal of a bottom card usually topples the whole structure. We recognize that neither life nor death is a singular state, but is organized and structured into levels.

Results of aggregation

The aggregation of living matter into a hierarchy of levels has a number of consequences. Thus, as already noted, *energy* must be expended to create a higher organizational level. Energy must also be supplied thereafter to maintain the organization. For example, if the energy supply to the cell, the organ, or the organism is stopped, death and decomposition soon follow and reversion to lower levels occurs. Similarly, maintenance of a family or a society requires work, over and above that needed to maintain the organization of subordinate units.

With each new level attained, the energy expenditure nets new properties. One of these is united, integrated function: nonaggregated structure means independent function and, by extension, competition; aggregated structure means joint function and, by extension, cooperation. Atoms, for example, may remain structurally independent, and they may then be in functional competition for other suitable atoms with which they might combine. Once they do aggregate into a molecule, they have lost structural independence and cannot but function unitedly, as a single cooperative unit. Similarly, cells may remain independent structurally, and they may compete for space and raw materials. But if they combine into a tissue, they surrender their independence and become a cooperative, integrated unit.

This generalization applies at every other organizational level as well. The results on the human level are very familiar. Men may be independent and competing, or they may give up a measure of independence, form families and societies, and start cooperating. Note here that sociological laws governing human society are based on, and are reflections of, the more fundamental laws governing the organization of all matter, from atoms to the whole living world.

Note also that competition and cooperation are not in any basic sense willful, deliberate, planned, or thought out; atoms or cells neither think nor have political or economic motives. Structural units of any sort simply function, as their internal makeup dictates. And the automatic result of such functioning among independent units may be competition; among aggregated units, cooperation. To be sure, human beings may decide to compete or to cooperate, but this merely channels, reinforces, makes conscious, and is superimposed on what they would necessarily do in any event. Reasoned cooperation is the most recent result of the ancient aggregative tendency of matter, and the evolution of reason may be regarded as nature's way of ensuring the possibility of a very close cooperation among organisms.

An important consequence of cooperation is operational efficiency. For the cooperating aggregate is more efficient in performing the functions of life than its subordinated parts separately and competitively. For example, a given number of separate cells must expend more energy and materials to survive than if that same number of cells were integrated into a tissue. Similarly for all other organizational levels.

The underlying reason for this difference is that, in the aggregate, duplication of effort may be avoided. Thus, in a set of separate cells, every cell is exposed to the environment on all sides and must therefore expend energy and materials on all sides to cope with the impact of the environment. However, if the same cells are aggregated into a disk or a ball, only the outermost cells are in direct contact with the environment, and inner cells then need not channel their resources into protective activities.

In one such form or another, savings in energy and materials, and corresponding gains in efficiency, almost always result from aggregation. If energy is the price paid to create and maintain higher organizational levels, then the return is greater efficiency and less waste, hence comparatively cheaper operation. This basically is what has favored more and more aggregation in matter generally and in living matter particularly. And this is why evolution has produced multicellular organisms rather than only bigger and better unicellular organisms.

Specialization

A further important consequence of cooperation is specialization. We may illustrate this by contrasting unicellular and multicellular organisms, but note that the basic principles hold for any level of organization.

A unicellular organism carries out all metabolic and self-perpetuative functions within the limits of its minute bit of protoplasm. In many instances, the performance of even one function requires most or all of the capacities of the cell. For example, in a bacterium, an ameba, or a single-celled alga, the *entire* cell surface is designed to serve as gateway for entering raw materials and departing wastes. The *entire* substance of the cell functions to distribute materials within it. And *all* parts of the cell may be required directly in locomotion or in feeding, for example (Fig. 3.5).

Very often, therefore, two such functions cannot be performed at the same time. In an ameba, because locomotion and feeding *each* necessitate action by the *whole* cell surface, performance of one of these functions more or less precludes the simultaneous performance of the other. Moreover, reproduction too involves the operational equipment of the *whole* cell, and in an ameba this necessitates temporary suspension of both feeding and locomotion.

Mutual exclusion of some functions by others is a common occurrence in all unicellular forms. That such an arrangement is nevertheless successful is proved by the existence of a multitude of single-celled organisms today. However, that such an arrangement is not particularly efficient is shown by the abundance of existing multicellular forms, which have an improved functional design. For in a cooperating aggregate, all cells need not carry out all functions. Instead, some cells may channel all their resources into performing one function, other cells into performing another function, and the total work may be divided up in this manner among the many available cells. Subdivision of

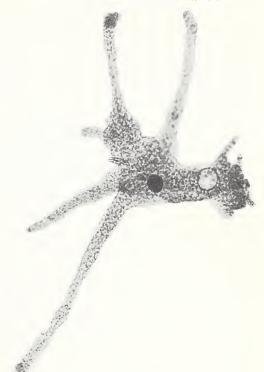


FIG. 3.5. An ameba. Like all other unicellular organisms, this one too carries out all metabolic and self-perpetuative functions within the confines of its single cell. Note nucleus (dark central body), excretory vacuole (light spherical body), and the pseudopods, i.e., fingerlike extensions which function in locomotion and feeding. (Carolina Biological Supply Co.)

labor enables each cell to become a *specialist* in one or a few jobs, and it performs these for the benefit of the whole aggregate.

For example, in the multicellular system some cells (e.g., gut cells) may become specialized to acquire food, for themselves as for all other cells. These other cells then need not perform that function but may concentrate their energy into carrying

out other specialized jobs. Some of the cells may develop particular sensitivity to stimuli and, as specialized sensory cells, may then serve in a manner beneficial to the whole aggregate. Analogously for other vital activities. This not only avoids duplication of effort, but each effort is carried out without dilution by parallel efforts, hence can be performed more cheaply.

In the multicellular organism, therefore, the individual specialized cell does not, and indeed *cannot*, perform all the functions necessary for survival. This is why, when some cells are separated away from the whole organism, as in injury, for example, such cells must usually die. We note that the gain in efficiency in multicellular systems is paid for not only by loss of cellular independence, but also by loss of cellular *versatility*. The specialized cell has lost independence mainly *because* it is not very versatile, because it can do only some of the many jobs necessary for survival. But the whole multicellular system, composed of many differently specialized cells, is still versatile as well as efficient.

The actual construction of a multicellular organism reflects these principles of division of labor and specialization. *All* cells of a multicellular organism are more or less specialized for given functions. Indeed, as noted above, cells with like specializations are arrayed into distinct tissues, and each tissue carries out usually just one main activity toward survival. Tissues in turn are arranged into more complexly *specialized* organs, and organs in their turn into *specialized* organ systems. A maximum number of such organ systems, namely, ten, is encountered in advanced modern animals:

The integumentary system, including skin and skin appendages, serving as outer cover and protective device for the whole organism

The circulatory, breathing, and excretory systems, which ferry foods, gases, and wastes between skin and the interior and within the interior

The alimentary system, which processes available foods into usable ones

The skeletal and muscular systems, which provide support, protection, and the means of motion

The reproductive system, which propagates the multicellular individual

The nervous and hormone-producing **endocrine** systems, which coordinate the activities of all organs and systems into a harmonious pattern

In different organisms, some or others of these systems are not present. For example, plants are without alimentary, breathing, excretory, muscular, and nervous systems: plants photosynthesize food, hence need not move to find it, and as we shall see, hormonal coordination suffices in plants, and gas transport and excretion can be accomplished on the tissue and organ level.

In this structural characterization, we have found organisms to be ordered, organized aggregates above a certain level of complexity, carrying out functions of metabolism and self-perpetuation at every level. Maintenance of the living levels requires energy, and this expense produces some loss of independence and versatility of the subordinate units, but also cooperation and gains in efficiency, through division of labor and specialization.

By virtue of the specialization of its cells, tissues, organs, and systems, the entire multicellular organism is itself specialized. It is a dependent, necessarily cooperating member of a larger living fabric: the social group, the whole species, the community of several species, the physical environment which encompasses all. Even man is so specialized. He requires a terrestrial environment of particular properties, a social community of variously specialized human beings, a community of wheat, cattle, and other food organisms. Thus the specializations of his body allow him to pursue no other but a characteristically human mode of life.

We conclude, therefore, that the large result of cellular specialization is adaptation of the whole organism: the ability to live in a particular biological and physical environment and the ability to pursue a particular way of life within that environment.

This leads us to our next topic, namely, an examination of the place of the individual organism within larger aggregations of organisms.

REVIEW QUESTIONS

- 1. What are the main types of organisms in existence today, and what distinguishes these from one another?
- 2. What is metabolism? Self-perpetuation? What are the principal component functions of each of these, and what specific roles do these functions play toward the maintenance of life?
- **3.** What are the fundamental differences between inanimate and living systems?
- 4. Define organisms, living, cellular specialization, death.
- 5. Review the hierarchy of levels in the organization of matter, and discuss how living matter is characterized in terms of levels.

- 6. Review the relationship of levels of organization to aggregation, competition, cooperation, and operational efficiency.
- 7. In terms of cellular specializations, how does a cell of a single-celled organism differ from a cell of a multi-cellular organism?
- 8. What are the functional advantages of high and of low degrees of specialization? Cite examples of specialization on the organism, society, species, and community levels of organization.
- 9. What are the organ systems of man, and which familiar organs belong to each of these systems?

SUGGESTED COLLATERAL READINGS

- Bonner, J. T.: The Social Amebae, Sci. American, vol. 180, 1949.
- ----: Volvox, a Colony of Cells, Sci. American, vol. 182, 1949.
- Holmes, S. J.: How Life Becomes Complex, in I. W. Knobloch, "Readings in Biological Science," Appleton-Century-Crofts, 1948.
- Kemeny, J. G.: Man Viewed as a Machine, Sci. American, vol. 192, 1955.
- Young, R. T.: The Living Machine, in I. W. Knobloch, "Readings in Biological Science," Appleton-Century-Crofts, 1948.

CHAPTER 4

Species and community

Being a specialized entity, every organism depends on other organisms for some essential product or process; no organism can survive entirely by itself. Cooperative aggregations of organisms are as ancient as organisms themselves, and as the ones evolved, so did the others. Moreover, the same principles and consequences of aggregation described previously for the levels below the organism hold also for the levels above.

In this chapter, we shall deal with two major levels above the organism, the species and the community. As one of the specialized groupings under the species level, we shall also examine the society, and as one of the expressions of community living, we shall discuss parasitism and other socalled symbiotic associations.

THE SPECIES

The nature of a species

Individual organisms of the same kind are grouped into a series of organizational units. The smallest such unit is the family, a rather temporary type of association and also a comparatively rare one, for it is found only among certain vertebrates. Also more or less temporary, and typical of only certain organisms, are the larger associations of families of the same kind into **tribes** and of tribes of the same kind into **societies**. But whether or not like organisms form families, tribes, and societies, they always form a next higher grouping, namely, local **populations**.

A population is a relatively permanent association of organisms of the same kind, encountered among all types of organisms. The dandelions in a field, the pines in a forest, the earthworms in a plot of soil, the minnows in a pond, and the people in a village, all are examples of local populations. Individual organisms multiply and die, emigrate or immigrate, but collectively the population persists. It may split into subpopulations, or it may fuse with adjacent sister populations, yet the basic character of the group as a whole does not thereby change. Structurally, the geographic extent of a population may vary vastly, from the space in a laboratory test tube to the space of a continent or an ocean. Functionally, the fundamental unifying link of a population is that its members interbreed more or less preferentially with one another. However, occasional interbreeding with members of sister populations does occur. A population thus is a reproductively closely knit unit, associated more loosely with similar sister units.

The sum of all the populations of the same kind, and thus the sum of all the organisms of the same kind, forms a species. For example, all the corn plants on earth, all the bullfrogs on earth, all the human beings on earth, each group represents a species. Even more so than the population, the species is a universal, very permanent grouping.

The identifying feature of a species is that the member organisms interbreed only with one another and not with members of other species. Thus, whereas cross-mating occurs more or less freely within a species, it does not occur at all between species. For example, bullfrogs from any part of the world may mate with bullfrogs from any other part. Similarly, grass frogs may mate with other grass frogs—and only grass frogs. But even though bullfrogs and grass frogs may, and often do, inhabit the

same pond, they never interbreed. They represent two different species.

Evidently, some kind of reproductive barrier exists between species. In many cases, as between bullfrogs and grass frogs, the barrier is biological, and interbreeding then is impossible regardless how close the organisms are. Thus bullfrogs and grass frogs have incompatible structures and functions, and sperms from one cannot successfully fertilize the eggs of the other. In numerous other cases, the eggs and sperms of different species are compatible, yet effective biological barriers still exist. For example, the breeding season in one group may occur a few weeks earlier or later than in another, or the members of one group may be active only at night, those of another only in the daytime. Interbreeding will be impossible under such circumstances.

In still other instances, the reproductive barriers are not biological but environmental. Impassable mountains, unfordable rivers, pronounced climatic differences, or merely great distances between one territory and another may make contact between

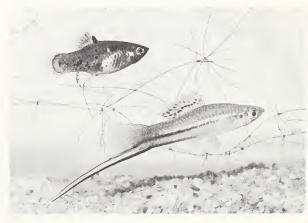


FIG. 4.1. Platyfish female at top, swordfish male at bottom. These animals belong to different species, and in nature they do not interbreed. But they can and do interbreed in the laboratory. (Courtesy of Dr. Myron Gordon and the Genetics Laboratory. New York Zoological Society.)

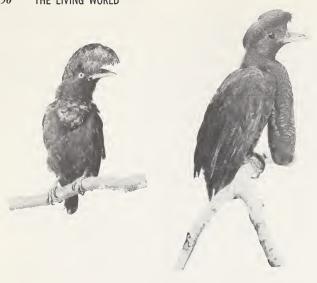


FIG. 4.2. Individual variation. These two umbrella birds belong to the same species, namely, Cephalopterus ornatus. But they are members of different populations and the structural differences between the birds are quite pronounced. Technically, these birds are said to belong to different subspecies of the same species. (New York Zoological Society.)

groups impossible, and reproductive isolation will be the consequence. Interbreeding can still occur if the isolating condition is removed, but in nature this does not normally happen. Evidently, when two different species do not interbreed in nature, this does not necessarily mean that they cannot interbreed. In many cases, members of different species may be brought together in the laboratory, and there they interbreed perfectly well. For example, swordtails and platys, two species of tropical fish (Fig. 4.1), may have offspring in the laboratory quite readily. But in nature they almost never do, because they normally live in different parts of a river and simply do not meet.

The development of new environmental isolating conditions is the usual cause of speciation, that is, the origin of new species by the splitting of one into two. For example, if an original parent species ranges over a given large territory, physical barriers may arise in the course of time which may prevent interbreeding between populations at opposite ends of the territory. With reproductive contact so lost, evolution in the now isolated populations may

henceforth follow entirely different courses. In effect, the parent species will be split into two new ones. At first, the two offspring species will still be rather similar structurally and functionally. In time, however, evolutionary changes are likely to introduce progressively pronounced differences, including biological barriers to interbreeding. These would add to, and reinforce, the environmental ones already in existence. Speciation by this means is the principal way in which new species evolve. Such a process takes, on an average, about one million years (see also Chap. 23).

Variations

Within a species, the member organisms all share a basic set of structural and functional characteristics. For example, no matter in what way or to what degree human beings might differ, they never differ so much that their human status cannot be recognized. Note, however, that there always are differences, and indeed no two organisms are ever exactly alike. We say that the organisms within a species exhibit individual variations (Fig. 4.2).

Two classes of variations may be distinguished, inheritable and noninheritable ones. The first are produced by gene mutations and are controlled by genes. They may therefore be transmitted to offspring. Noninheritable variations are the result of developmental processes within organisms and are not controlled genetically. For example, if a man is an athlete, his muscular system is likely to be developed much more than in the average person. This is an individual variation and a noninheritable one. For the degree of muscular development does not depend on heredity, primarily, but only on whether or not a person goes in for athletics. On the other hand, the blood type, the skin color, the hair color, and the sexual nature of an individual as male or female are examples of hereditary variations. They are part of the genetic inheritance from parents and earlier forebears and will, in turn, influence the traits of future offspring generations (Figs. 4.3 and 4.4).

In many, and probably in the majority, of instances, the variations within a species are correlated with variations in the environment. Among birds and mammals, for example, man not excepted, clear-cut structural differences accompany differ-

ences in climatic temperatures. In warm climates, for example, individuals of a species tend to have smaller body size, longer ears, tails, and other protrusions, and darker body colors than fellow members of the species living in cold climates. Such structural variations are said to be adaptive; that is, they are advantageous to the individuals in the different environments. Smaller bodies and longer ears, for example, make for a large body surface relative to the body volume. Under such conditions evaporation from the skin surface is rapid, and the cooling effect of this enhanced evaporation is of considerable benefit in a warm climate. Conversely for the cool climate. In many instances it may be very difficult to recognize the adaptive value of a variation. And some variations conceivably may be nonadaptive, without inherent advantage to the possessors. Human eye color may possibly be in this category.

Variations within a species may be exceedingly pronounced. Two individuals may be so different structurally and functionally that their common traits become evident only through the most careful study. Familiar examples of this are found in insect societies. These often consist of kings, queens,

FIG. 4.3. Inheritable variations. These are litter-mate rats, produced by the same two parents. Considerable variation in coat color is evident. Such differences arise because even brothers and sisters of the same family may be different genetically. Hereditary (i.e., gene-controlled) variations tend to be the more pronounced, the less related the given members of a species. (American Museum of Natural History.)

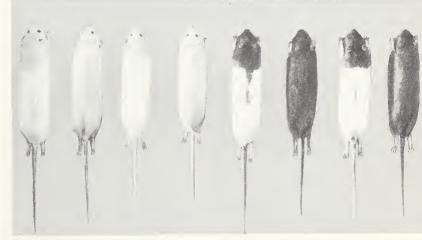




FIG. 4.4. Courtship of fur seals. Female on left, male on right. Sexual variation is illustrated strikingly here, the male being far larger and darker than the female. (Courtesy of V. B. Scheffer, U.S. Fish and Wildlife Service.)

drones, soldiers, workers, and other "castes," all structurally and functionally very dissimilar (see below).

Such instances of great variation indicate a high degree of *specialization* of individuals. In insect societies, for example, each of the different types of individuals is specialized to perform only certain jobs and the survival of the society depends on the cooperation of the different members. In one form or another, a high degree of individual variation and specialization is always characteristic of societies, as the following section will show.

THE SOCIETY

A society is subordinated to both the species and the population; it is a grouping of organisms within a population. Where social groups occur, ties of heredity, function, and tradition are strong, and these usually limit the reproductive contact with other societies of the population. Tribal and family units may or may not occur within a society.

Societies are characteristic only of animals. Also, all societies have evolved independently of one another, and the most advanced societies occur in the most advanced animals: insects and vertebrates.

Insect societies

Highly developed societies occur among termites, ants, bees, and wasps. In these, each member organism is structurally adapted from birth to carry out specific functions in the society. Insect societies, organized somewhat differently in each of the four groups just named, operate in fixed, stereotyped, largely unlearned behavior patterns. In its rigid, inflexible ways, the insect society resembles a human

dictatorship, except that among insects there is no dictator, no rule by force. Each member is guided by inherited, instinctive reactions, unable to carry out any functions other than those for which built-in instincts exist. Insects can learn, though only to a limited extent. For example, a bee may be taught to respond differently to different colors and scents, and it may learn a new route to its hive if the hive has been moved.

Social insects have this in common: they build intricate nests, and their societies are stratified into structurally distinct castes (Figs. 4.5 and 4.6). In each of the four groups, different species form societies of different degrees of complexity. A quite complex society is encountered among honeybees.

A colony of honeybees (Fig. 4.7) is made up of three social ranks: a queen, tens or hundreds of male drones, and from 20,000 to 80,000 workers. The queen and the stingless drones are fertile, and their main functions are reproductive. The smaller-bodied workers are all sterile females. They build the hives, ward off enemies, collect food, feed the queen and the drones, and nurse the young.

When a hive becomes overcrowded, the queen together with some drones and several thousand workers secedes from the colony. The emigrants swarm out and settle temporarily in a tree or other suitable place until a new hive is found (Fig. 4.8). In the old hive, meanwhile, the workers which remain behind raise a small batch of the old queen's eggs in large, specially built honeycomb cells. These eggs develop into new queens. The first one to emerge from its cell immediately searches out the other queen cells and stings their occupants to death. If two queens happen to emerge at the same time, they at once engage in mortal combat until one remains victorious. The young queen, her succession now undisputed, soon mates with one of the drones. In a nuptial flight high into the air, she receives millions of sperms which are stored in a receptacle in her abdomen. The sperms from this single mating last through the entire egg-laying career of the queen.

Among the eggs laid individually into honeycomb



FIG. 4.5. A queen ant. (Ward's Natural Science Establishment, Inc.)

cells some escape fertilization, even in a young queen. None is fertilized in an older queen once her sperm store is exhausted. Unfertilized eggs develop into drones. Fatherless development of this sort, or natural parthenogenesis, is widespread among social insects and a number of other animal types, e.g., rotifers, water fleas, brine shrimp. Fertilized eggs develop into larvae, and these either into queens or into workers, depending on the type of food the larvae receive from their worker nurses. Larvae to be raised into workers are fed a "regular" diet of plant pollen and honey. Queens form when the larvae receive an especially rich "royal jelly," containing pollen, honey, and comparatively huge amounts of certain vitamins. But new queens are not raised while the original queen remains in the hive, healthy and fertile. If the queen produces eggs faster than honeycomb cells can be built, she receives less food from her attendants. Egg production then slows. Conversely, if she is behind in her egg laying, she is fed more intensively (Fig. 4.9).

In the six weeks or so of its life, a worker bee does not perform the same duties continuously. The age of a bee determines what work it can do: housekeeping tasks are performed by young bees; foodcollecting trips are made by older ones. On a foodcollecting trip, the bee gathers pollen, rich in pro-



FIG. 4.6. Portion of termite nest. In central chamber note queen, her abdomen swollen with eggs, being cared for by workers. Winged king in lower right corner, larval queen in upper left corner. (Courtesy of C. E. Simmons, Buffalo Museum of Science.)

tein, and nectar, a thin sugar solution. Pollen is carried home in *pollen baskets* on the hind legs. Nectar is swallowed into the *honey crop*, a specialized part of the alimentary tract, where saliva partially digests the sugar of nectar. On arriving at the hive, the bee first passes a security check on the way in, then unloads its pollen into one cell and regurgitates its nectar into another. Other bees which happen by pack the pollen tight and start

converting nectar into honey. They rapidly beat their wings close to a nectar-filled cell, a process which is continued until most of the water has evaporated. Every now and then a bee samples the product (probably more a matter of hunger than of professional pride in the work). And when the honey is just right (or when all the bees standing by have had their fill?), the cell is sealed up with wax. This is the principal food store for the winter.

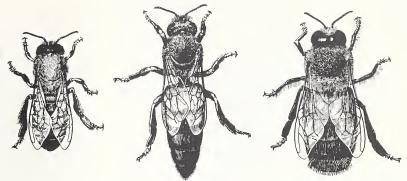


FIG. 4.7. Honeybees. Worker on left, queen in middle, drone on right. (U.S. Department of Agriculture.)

Pollen is unobtainable at that time and, being perishable, cannot be stored as readily.

Bees, and other social insects as well, possess remarkable powers of orientation and communication. On food-collecting trips, bees have been shown to navigate by the sun. They are able to relate the position of their hive with the direction of polarized light coming from the sun; hence they may steer a beeline course home from any compass point. On arrival in its hive, a scouting bee which has found a food-yielding field of flowers communicates with its fellow workers by means of an abdominal dance, a side-to-side wiggle of the hind portion of the bee's body. The violence of the dance gives information about the richness of the food source. Flight distance is indicated by the duration of the dance, and flight direction, by the specific body orientation the dancing bee assumes on the honeycomb surface.

In winter, bees cling together in compact masses. Animals in the center always work their way out; those near the surface work their way in. A clump of bees thereby withstands freezing, even when exposed to very low temperatures. Smoke calms bees, as is well known. The animals react to smoke by rushing to their food stores and gorging themselves with honey. They are too busy at that time to sting an intruder. This is probably an inherited adaptive response to fire. Smoke might indicate a burning tree, and it is of obvious advantage if the

FIG. 4.8. A swarm of bees, emigrated from a parental hive and searching for a new hive. (U.S. Department of Agriculture.)







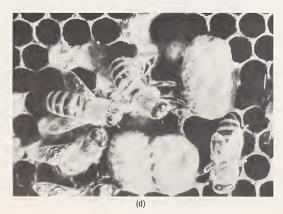




FIG. 4.9. (a) Queen bee laying eggs, surrounded by attendants. (b) Nurse bee feeds and cleans the larvae in the brood cells. (c) A worker bee just hatching out from its brood cell. (d) Two enlarged brood cells, capped over with wax, in which queen bees are being raised. (All photos copyright © Walt Disney Productions.)

bees are well fed when they are forced to abandon their nest. Similarly adaptive is the expulsion of all drones from the colony at the approach of winter; not contributing to the well-being of the colony, males merely use up food which is at a premium in the cold season. Reactions such as these might appear to be thought out. Yet bees probably do not "reason" at all (Fig. 4.10).

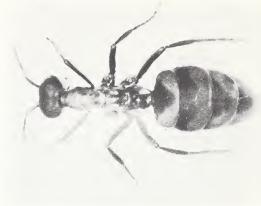
Among insect societies generally, the fixed nature of each individual constitutes a potential long-range disadvantage. For example, death of a queen bee and destruction of honeycomb cells which contain larvae still young enough to be reared into queens usually spell the end of a bee colony. For new workers are not produced, and old ones die out. Destructive social crises of this sort are offset by the establishment of numerous colonies and by enormous reproduction rates. The safety of the species lies in the number of its individuals. We recognize, however, that it would be immediately advantageous if, in addition to safety through num-

bers, the society were organized more flexibly; if each member could perform the functions of every other member and if the colony as a whole could learn to adopt new ways of life in the face of changed environmental conditions. Flexible social organization is actually in evidence to greater or lesser degree among vertebrate groups.

Vertebrate societies

In contrast to insects (and disregarding the differences between males and females), the members of vertebrate societies are more or less alike at birth, structurally. Individual variations largely develop later, and they are not primarily structural as in insects, but functional. Thus they may involve variation in physical strength, in developed skills, in mental capacity, and in some cases in social tradition. As in insects, on the other hand, the main determiner of behavior is inherited instinct. tempered here with a more or less thin veneer of learning and reasoning. Learning goes hand in hand with training, and both are made possible largely by family groupings. The subdivision of the advanced vertebrate society into family units is one of its main distinctions.

Schools of fish, flocks of birds, packs of European wolves, herds of deer are some of the most primitive of the associations among vertebrates. Functional variation of individuals is not particularly pronounced here. In travel, the individual which happens to be in the lead position, usually a male, guides the group temporarily. Other males, often stationed along the outskirts of the group, may take the lead in frequent rotation. The advantages of such associations are largely protective. Many eyes see more than two; a closely huddled herd stays warm; a group is more effective in attack and in defense. Family life within such groups may or may not be evident. There is hardly any in schools of fish. But a duck or a doe trains its young. Families tend to maintain their own physical space within the society. For example, in a herd of seals resting on an island, males take up stations at more or less regular intervals and each male gathers his family



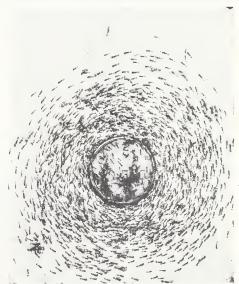


FIG. 4.10. Army ants. One photo shows queen, the other a marching column. If such a column is made to travel in a circle, as in the photo, then these ants will continue to circle endlessly. Unless they are diverted by an outside force, they may march themselves to death. Each ant evidently is governed by inherited instinct so completely that it is capable only of following the ant before it and incapable of thinking itself out of an even slightly altered situation. (American Museum of Natural History.)

around him. The individual patriarch jealously guards his territory, driving off bachelor males and keeping a sharp eye on his females (Fig. 4.11). Social life among beavers is more cooperative and rather more advanced. Several families may pool their efforts in woodcutting and dam building. All share the benefits of this teamwork, which clearly serves more than mere protection.

Social herding very often is associated with extensive animal migrations. These may be undertaken in search of richer or safer pastures, in response to seasonal changes in climate, or to reach geographically fixed breeding grounds. Eels, seals, salmon, and many types of birds are among familiar migrants. When not migrating, solitary individuals or families of these animals may be dispersed widely over a considerable territory. At specific times, as if on cue, individuals draw together from far and near

FIG. 4.11. Fur seals on an island in the far north. This group illustrates the familial organization of the typical vertebrate society. The social unit is composed of a single male (dark animal at back), several females, and their young. (Courtesy of V. B. Scheffer, U.S. Fish and Wildlife Service.)



to a common jumping-off point, and then they travel together to their destination, as a band.

Not all vertebrate societies migrate, and not in all cases are families grouped into herds. Solitary families are common, among both monogamous and polygamous species. Fish such as sticklebacks, birds such as parrots, and mammals such as bears and wolverines are monogamous and may mate for life. Such family groups are organized like human families.

Solitary polygamous families may approach the numerical proportions of flocks or herds, as in chickens. Such a group is usually made up of a single dominant male, a series of females, their young, and sometimes a few unrelated young bachelor males. The rule of the dominant male is frequently challenged by the bachelors. If one of these succeeds in defeating his opponent in battle, the loyalty of the females is transferred to the winner. In this way the group is assured of continuously fit, healthy leadership.

An interesting social organization exists among the females of a polygamous family. In a flock of chickens, for example, hens are ranked according to a definite peck order. A given hen may peck without danger all hens below her in social rank but may be pecked in turn by all hens above her in the scale. If a new hen is introduced into the flock, she undertakes, or is made to undertake, a pecking contest with each fellow hen. Winning here and losing there, she soon finds her level in the society. A high ranking carries with it certain advantages, such as getting first to the food trough and obtaining a position of prestige on the perch. Very high ranking birds often are so aggressive that they persistently reject the attentions of the rooster. More submissive hens then produce most of the offspring. Social ranking of a similar nature is found also among female elephants as well as in most other polygamous families.

The success of vertebrate societies as a whole lies primarily in the functional versatility of the individual. In the insect society, as we have noted, reproduction of the majority is suppressed and reproduction of the minority serves not only toward the new formation of individuals, but also toward the new formation of the whole society. Thus, among insects, the fate of the society hinges on the fate of a single female and her genes alone provide continuity from one social generation to the next. By contrast, virtually all members of a vertebrate society are reproducers. Social continuity consequently is the responsibility of many, and reproduction of any one individual is less vital for the propagation of the society.

Although insect and vertebrate societies differ in origin and internal organization, remarkably similar patterns of social behavior are in evidence. For example, ant societies exist which make deliberate war, others which practice slavery, and still others which pursue agriculture and domesticate other organisms. Such ants and man are unique in these respects among animals.

Society in all its forms is subordinated to the larger local population and to the still larger species. Populations of social and nonsocial organisms in turn are subordinated to the local community, an aggregation that occupies our attention next.

THE COMMUNITY

A community is a local association of populations of several different species. A pond with its various plant and various animal populations is a community; so is a forest, a meadow, a section of ocean shore, or a village with its people, trees, grasses, bacteria, cats, dogs, and other organisms. The sum total of all communities makes up the whole living world.

The boundaries between communities are not primarily biological, as between species, but are primarily geographical and environmental. And the *kind* of community likely to be found in a given territory depends largely on the physical and chemical nature of that territory. For this reason, we shall discuss the different specific types of communities in the next chapter, in a context which stresses the environmental aspects of the living world.

Here we shall deal with the general characteristics of all types of communities and with the forces which govern their structure.

Cycles and balances

Like other living entities, a community grows, develops, passes through a relatively stable mature phase, reproduces and ultimately dies. The time scale is in hundreds and thousands of years.

Such communal life cycles result from an interplay between organisms and their environment. Being specialized, different organisms are adapted to, and must therefore live in, different environments. The physical character of a given region consequently determines what types of organisms can settle there originally. Temperature, winds, amount of rainfall, the chemical composition of the surroundings, latitude and altitude, soil conditions, and other similar factors decisively influence what kinds of plants will be able to survive in a given locale. Vegetation, in turn, as well as the physical character of the locale, has a selective effect on the types of animals that may successfully settle in the region.

By its very presence, however, a given set of organisms gradually alters local conditions. Raw materials are withdrawn from the environment in large quantities, and metabolic wastes are returned. To the extent that these wastes differ from the original raw materials, the environment becomes altered. Moreover, the parts of dead organisms also return to the environment, but not necessarily in the same place, nor necessarily in the same form, in which they were obtained. In time, organisms thus bring about profound redistributions and alterations of vast quantities of the earth's substance.

This means that later generations of the original organisms may find the changed local environment no longer suitable, and the members of the community must resettle elsewhere or die out. A new community of different plants and animals may come to occupy the territory, and as this community now alters the area according to its own specialization, type replacement, or communal succession,

may eventually follow once more. We note how closely the nonliving and the biological parts of the environment are interlinked; change in one produces change in the other.

Communal succession of this sort may ultimately lead to the establishment of a climax community: a set of organisms which alters the local environment in such a way that the original conditions are repeatedly re-created more or less exactly. The North American prairie and forest belts are good examples of climax communities; so are the communities in deserts, large lakes, and in the ocean. Such associations are relatively stable, and they continue to exist within a territory as long as local conditions are not altered drastically by climatic or geological upheavals. If that happens, communal death usually follows. Development of new communities by immigration or major evolutionary adjustment of the remnants of the old community may then occur.

In a community, as on all other levels of living organization, *turnover* occurs continuously; individuals of the various populations emigrate or die out and are replaced by others. The important point is that, in a climax community, this flux is automatically self-adjusting, so that the community

remains internally balanced and exhibits a numerical steady state; that is, in all populations present, the numbers of individuals remain relatively constant. In a large, permanent pond, for example, the number of frogs, minnows, and any other organisms, plant or animal, will be more or less the same from decade to decade. Annual fluctuation is common, but over longer periods of time, constancy of numbers is characteristic in most natural communities.

Control factors

What creates and controls these striking numerical balances? Three main agencies do so: food, reproduction, and protection, the three principal links which make the members of a community dependent on one another.

In every stable community, plants photosynthesize their own food; herbivorous animals eat the plants; carnivorous animals eat each other or herbivores; the elimination products and the dead bodies of all plants and all animals replenish the ocean or the soil; and this, plus solar energy and raw materials from the environment, then makes new plant growth possible (Fig. 4.12).

In such cycles, a pound of food eaten by an

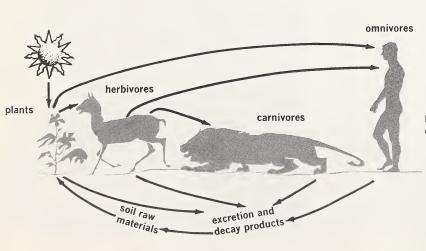


FIG. 4.12. The basic nutritional links in a community.

animal does not make a pound of new animal protoplasm. Much of the food is water; some components are indigestible altogether; some escape digestion in their passage through the gut. Nor is the total energy content of a pound of food actually usable in metabolism, since loss of energy in the form of heat cannot be avoided. Therefore, when one organism eats another, this transfer of protoplasm is not 100 per cent efficient. *More* than 300 lb of antelope meat, or even lion meat, is required to produce a 300-lb lion.

This inescapable condition leads to the establishment of food pyramids in the community (Fig. 4.13). So many tons of soil can support only so many fewer tons of grass. Grass in turn supports herbivores which together weigh less than the grass. And only a relatively small weight of carnivores can find sustenance in such a community. Several acres of ground thus might just be enough to support 150 lb of human protoplasm.

Note that such a pyramid of total weights also describes a pyramid of individual numbers and individual sizes. For prey is generally smaller than predator. Hence the balanced community may contain millions of individual grasses, but only one man.

Pyramids of this sort are one of the most powerful factors in balancing communal populations. For significant variations of numbers at any level of a pyramid bring about automatic adjustments at every other level. For example, overpopulation of carnivores soon results in the depletion of herbivores, since a greater number of herbivores is eaten. This depletion leads to starvation of carnivores. hence reduction of their numbers. Underpopulation of carnivores then results in overpopulation of herbivores, since fewer herbivores are eaten. But the fewer carnivores can be well fed; hence they may reproduce relatively rapidly, and this increases their number again. The cycle then repeats. As a result, although the numbers undergo short-term fluctuations, they remain relatively constant over the long term.

The reproductive interdependence within a com-

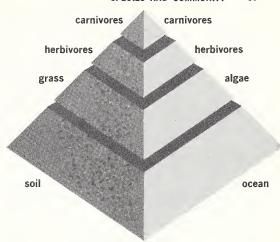


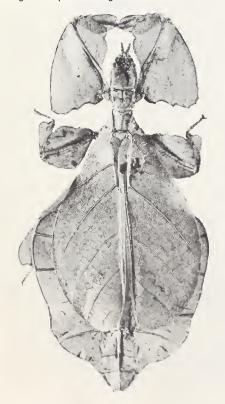
FIG. 4.13. The general pattern of food pyramids. Soil and ocean support photosynthesizing forms, herbivorous animals subsist on the photosynthesizers, and carnivorous animals subsist on the herbivores.

munity is illustrated clearly by the pollinating activity of insects. In some well-known cases of remarkable specialization, a given insect visits only one or a few specific flower types for pollen and nectar, and the flower in turn is structurally adapted to facilitate entry of the insect (e.g., the liplike petals of snapdragon flowers). Such intimate cooperation indicates that the animal and the plant have evolved together, in close correlation. It is fairly obvious how such interdependence contributes to population balance: reduction of the insect population brings with it reduced plant pollination, hence reduction of the plant population, and vice versa. Similarly significant in balancing the size of plant populations is the seed-dispersing activity of birds and mammals.

Other examples of reproductive dependence are many. Birds such as cuckoos lay eggs in nests of other birds. Insects such as gall wasps embed their eggs deep in the tissues of particular plants, where the hatching larvae find food and protection. Other insects deposit eggs on or under the skin of various animals. Certain wasps, for example, kill tarantulas and lay their eggs in them.

Numerous examples also give evidence of the protective interdependence of the organisms within a community. For instance, the many ways in which forests and grasslands house and hide large and small animals are commonplace. Protective devices here usually involve *camouflage* of body colors or of body shapes. Probably the most remarkable instance

FIG. 4.14. The shape of many insects mimics that of plant parts on which these animals habitually live. The photo shows a leaf insect whose resemblance to a leaf is exceptionally striking. (U.S. Department of Agriculture.)



of color camouflage is the phenomenon of mimicry, widespread particularly among butterflies and moths. In certain of these animals, pigmentation patterns exist which are virtually indistinguishable from those of other, unrelated species. Usually those species are mimicked which are strong or fast and have few natural enemies. The advantage is that an animal resembling, even superficially, another more powerful one will be protected too, by scaring off potential enemies.

Insects also display a variety of structural camouflages. For example, the individuals of certain species possess the detailed shape of leaves, of branches, or of thorns (Fig. 4.14). This serves not only defensively, but also as a disguise against potential victims.

Other protective devices vary widely in type. Various birds and some mammals mimic the song and voice of other species, either defensively or as an aggressive lure. The hermit crab protects its soft abdomen in an empty snail shell of appropriate size. Schools of small pilot fish scout ahead of large sharks, leading their protectors to likely prey. Significant protection is also provided by man, through domestication, game laws, parks, and sanctuaries.

In these and other similar instances, overpopulation reduces the relative amount of protection available against enemies or adverse climates. Through this, protective opportunities become powerful controlling factors of communal population balances.

These various considerations show clearly that the member populations of a community are specialized nutritionally, reproductively, and protectively. Thus carnivorous populations cannot sustain themselves on plant food and not even on every kind of animal food. Herbivorous populations require plants and are incapable of hunting for animals. The plant populations in turn depend on soil, and the populations of saprophytic bacteria cannot do without dead protoplasm. These are profound specializations in structure and function, and they imply loss of individual self-sufficiency, as well as a need for cooperative interdependence. Com-

munal associations of populations evidently are a *necessity*. They are but extensions, on a higher biological level, of the necessarily cooperative aggregations of cells into tissues, organs, and organisms.

Indeed, the development of "community" is as integral a part of evolution as the development of individual organisms. Events were *not* such that a particular organism first evolved structurally and functionally in a certain way and then happened to find the right community into which it could fit. Instead, the community existed from the very beginning, and all its member populations evolved *together*; the community itself evolved. The histories of the bumblebee and the snapdragon are linked as intimately as the histories of every man's hand and foot.

A community within a given territory includes not only organisms which live in loose cooperative association. It also includes organisms which live together in more or less permanent physical contact. Two individuals of different species may be joined so intimately that one lives right within the other. All such instances of physically intimate living together, of members of different species, are instances of symbiosis, a special form of communal life.

SYMBIOSIS

The pattern

A free association in which an animal habitually shelters under a plant might, in a relatively simple evolutionary step, become an association in which the animal and the plant have entered a more permanent protective union. A plant which depends on some animal for seed dispersal might advantageously live in, or on, the animal altogether, not only at the time of seed production, but throughout life. A soil bacterium, or a scavenging protozoon, living on the undigested elimination products of larger forms, might find a surer food supply if it could adapt to an existence right in the gut cavity of its supplier.

Among ancestral populations of free-living forms, ample opportunity existed for the development of such symbiotic relationships. These opportunities were exploited to the full, and many associations arose in which two organisms of different plant or animal species came to live together in intimate, lasting physical contact. Today there is no major group of plants or animals which does not include symbiotic species, and there is no individual plant or animal, man not excepted, which does not play host to at least one symbiont.

Symbionts affect each other in different ways. Thus mutualism describes a relationship in which both associated partners derive some benefit, often a vital one, from living together. Commensalism benefits one of the partners, and the other is neither helped nor harmed by the association. Parasitism is of advantage to the parasite but is detrimental to the host to greater or lesser extent. These categories intergrade imperceptibly, and in many boundary cases clear-cut distinctions cannot be made.

An example of a mutualistic association is the tickbird-rhinoceros relationship. The tickbird feeds on skin parasites of the rhinoceros, and in return the latter is relieved of irritation and obtains warning of danger when the sharp-eyed bird flies off temporarily to the security of the nearest tree.

Another example is the mutualistic symbiosis of sea anemones and hermit crabs. Sea anemones

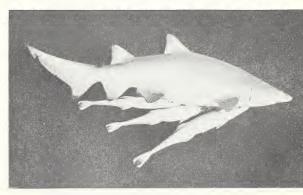
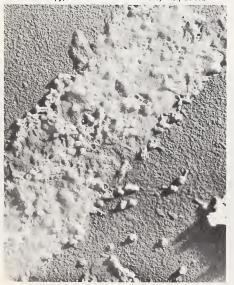


FIG. 4.15. Commensalistic symbiosis. Shark with three suckerfish attached to underside. (New York Zoological Society.)



FIG. 4.16. Mistletoe, parasitic on branch of pine tree. (U.S. Forest Service.)

FIG. 4.17. Electron micrograph of the remnants of a bacterium after attack by bacteriophages. The virus parasites are the small rodlets with knobbed ends. Bacteriophage viruses are also shown in Fig. 20.2. (R. W. G. Wyckoff, "Electron Microscopy," Interscience Publishers, Inc., 1949.)



attach themselves to empty snail shells, and hermit crabs use these shells as protective housing. The sea anemone, an exceedingly slow mover by itself, is thus carried about on the shell of the hermit crab—an obvious advantage to the anemone in its search for food and in geographic dispersal. The hermit crab in turn benefits from the disguise. Moreover, since the anemone is not a dainty eater, scraps of food become available to the crab when the anemone catches prev.

Mutualism is also encountered among animals which harbor billions of intestinal bacteria in the lower gut. The bacteria draw freely on materials not digested or not digestible by the host, and as a result of their activities, they initiate fecal decay (Chap. 11). The host generally benefits from the auxiliary digestion carried out by the bacteria and in many instances is also dependent on certain of the bacterial byproducts. For example, mammals obtain many vitamins in the form of "waste" materials released by the bacterial symbionts of the gut.

Commensalism is illustrated by a species of small tropical fish which finds shelter in the cloaca of sea cucumbers. The fish darts out for food and returns, to the utter indifference of the host. The so-called suckerfish (Fig. 4.15) possesses a dorsal fin which is modified into a holdfast device. By means of it, the fish attaches to the underside of sharks and thereby secures scraps of food, wide geographic dispersal, and protection. The shark neither benefits nor suffers in any respect. Barnacles may attach to the skin of whales, an association which secures geographic distribution and wider feeding opportunities for the sessile crustaceans. In this instance, a trend toward parasitism is in evidence. For in some cases the barnacles send rootlike processes into the whale, outgrowths which eat away bits of host tissue.

Parasitism is actually the most stable and most widespread form of symbiosis.

Parasitism

Parasitic ways of life. It has probably become apparent in the above that symbiosis revolves largely, though not exclusively, around the problem

of food. We might suspect, therefore, that symbiosis in general, and parasitism in particular, would be most prevalent among organisms in which competition for food is most intense. This is actually the case.

Although there exist occasional parasitic green plants (e.g., mistletoes, Fig. 4.16), photosynthesizing organisms by and large are not under competitive pressure for basic nutrients. For air, water, and sunlight are present everywhere, in inexhaustible quantities. Parasitism flourishes primarily among organisms which must obtain food from other protoplasm: in viruses, in bacteria, in fungi, and in animals.

All viruses are parasitic. Of the bacteria, those which are not chemo- and photosynthetic or saprophytic are parasitic. Among fungi, some are saprophytic, the rest are parasitic. And in animals, many major groups are wholly parasitic; virtually all others include important parasitic subgroups (Chaps. 7 and 9).

So advantageous and economical is the parasitic mode of living that many parasites may be infested with smaller parasites of their own, and these in turn may support still smaller ones. For example, a mammal may harbor parasitic worms; these may be invaded by parasitic bacteria; and the bacteria may be infected by bacteriophages, i.e., viruses which parasitize bacteria (Fig. 4.17). Hyperparasitism of this sort, i.e., one parasite inside another, is very common. It represents a natural exploitation of the very condition of parasitism. Inasmuch as the parasite is generally smaller than the host, and inasmuch as one host may support many parasites, parasitic and hyperparasitic relationships form inverted food pyramids, contained within the pyramids of the larger community.

The first problem a potential parasite faces is the defense mobilized by a potential host. Attachment to the outer body surface can be prevented only with difficulty, particularly if the host does not possess limbs (Fig. 4.18). Numerous ectoparasites exploit this possibility. Equipped with suckers, clamps, or adhesive surfaces, they hold onto skin

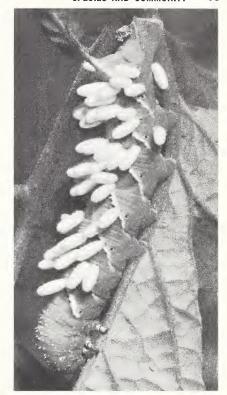


FIG. 4.18. A caterpillar of a sphinx moth, parasitized by the pupae of another insect species. (Courtesy of E. W. Teale.)

or hair, and with the aid of cutting, biting, or sucking mouth parts, or with rootlike outgrowths, they feed on the body fluids of the host. Examples: many fungi and leeches, lice, ticks, mites, and lampreys.

Endoparasites, within the body of the host, must breach more formidable defenses. Digestive juices and strong acids in the alimentary tract of a host, antibodies in the blood, white blood cells, and other cells which engulf foreign bodies in ameboid fashion, these are among the defensive agents which guard against the invader. Overcoming such de-

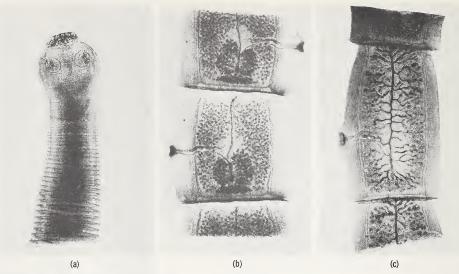


FIG. 4.19. Tapeworm. (a) Head. (b) Segmental sections near middle of body. (c) Segmental sections near hind end of body. Tree-shaped structures in (b) and (c) are reproductive organs. Note testes filling segments in (b) and genital pores opening on the sides of the segments. The uterus filled with eggs is conspicuous in (c). (General Biological Supply House, Inc.)

fenses means *specialization*: development of resistant outer coverings, as in bacteria and fungi; tough cuticles, as in most parasitic worms; development of cyst walls and capsules or of hooks or clamps with which to hold on to the gut wall; and development of enzymes which, when secreted, erode a path through host tissues.

Specialization of the parasite also involves the selection of *specific* hosts. Highly advanced parasites cannot pick a host at random, even if many similar ones offer the same type of food. During the evolution of a parasite, structural and functional specializations have developed in adaptation to particular hosts only.

Thus most parasites enter a host's body by fixed routes, then settle in fixed regions, as if, in the course of time, they had learned to channel their attack through points of weakness characteristic of particular hosts.

Once established in the body of a host, the parasite may pursue a life of comparative ease. Embedded in food, it needs no locomotor equipment, few sense organs, no fast nervous reflexes. Indeed, structural and functional degeneracy is a nearly universal characteristic of parasites.

Structural degeneracy is pronounced in *tape-worms*, for example. These parasites (Fig. 4.19) possess only a highly reduced nervous system, a reduced muscular system, and not even a vestige of a digestive system. Almost like blotting paper, the worms soak up through their body walls the food juices of the host gut.

Such degeneracy is probably an adaptive advantage. For the degenerate condition of the parasite may be more economical than the fully developed condition of the free-living ancestor. A tapeworm, for example, being structurally degenerate, may concentrate all its resources into parasitizing the

host, and it need not divert energy and materials into maintaining elaborate nervous, muscular, or digestive systems, which are unnecessary anyway in this parasitic way of life.

Parasite reproduction. In one respect parasites are far from degenerate: reproduction. In this function they are as prolific as the most prolific free-living forms. The practical necessity of this is correlated with a major problem confronting the parasite, particularly the endoparasite, namely, how to get from one host to another.

Parasites succeed in two ways, both of which involve reproduction: active transfer and passive transfer. In the former, one stage of the life cycle of the parasite is free-living and motile; that is, this active stage transfers from one host to another through its own powers of locomotion. For example, the adult may be parasitic, and the free-living embryo or larva may be capable of locomotion. Or the larva may be the parasite, the adult then being free-living and capable of locomotion.

Passive transfer is encountered among parasites in which no stage of the life cycle is capable of locomotion. Propagation here is accomplished by wind, by water, or by intermediate hosts. The last offer a means of transfer which is not quite as chancy as random distribution by wind or water. What is involved here is well illustrated in the propagation of tapeworms.

These parasites of man (Fig. 4.20), like numerous others, exploit one of the easiest routes into and out of the host, namely, the alimentary tract. Entering through the host's mouth by way of eaten food and leaving through the anus by way of feces, some, like tapeworms, spend their adult life directly in the gut cavity of the host. Others utilize the gut as a springboard from which to invade interior tissues. The problem is to transfer offspring from one human host to another by passive means. Tapeworms accomplish a first phase of this readily; namely, mature eggs are released to the outside with the host's feces.

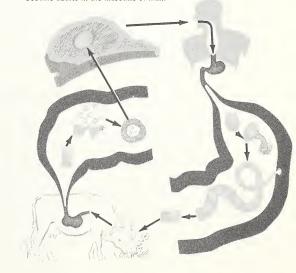
Since man does not eat feces, the eggs evidently

cannot reach new human hosts directly. However, tapeworms ingeniously take advantage of the food pyramids of which man is a member: man eats beef, and cattle eat grass. A ready-made pathway from grass to man thus exists, and the transfer chain becomes complete if, as happens on occasion, human feces are deposited on grass. Tapeworm eggs clinging to such vegetation may then be eaten by cattle.

In the intestine of a cow, a tapeworm egg develops into an embryo, and such an embryo bores a path through the gut wall into the cow's bloodstream. From there the embryo is carried into beef muscle, where it encapsulates and matures. If man then eats raw or partially cooked beef, the capsule surrounding the young tapeworm is digested away in the human gut, and the free worm now hooks on to the intestinal wall of its new host.

This history illustrates a very widely occurring

FIG. 4.20. The life cycle of a tapeworm. Ripe sections of the worm pass with the feces from the human gut. Eggs are released from these sections in the gut of cattle. Tapeworm embryos then encapsulate in beef muscle, and the embryos become adults in the intestine of man.



phenomenon. Many kinds of parasites utilize wellestablished food pyramids in transferring to new hosts. Often indeed there is more than one intermediate host, and by such means parasites have solved their transfer problems most successfully. So successfully, in fact, that now there are many more parasites in existence than free-living forms.

That parasites have shaped the course of human history at least as much as man himself is today recognized widely. That the parasitic way of life—not that of man, not that of the insect, not that of the plant—is really the dominant way on earth is even more significant. Man often holds parasitism

in utter contempt. In his ethical code it becomes a way of despicable insidiousness. But purely as a question of ethics, we may ask which is the more contemptible: predator man, who ruthlessly hunts down his victim as a matter of "necessity"; the "gentle" herbivore, who tramples a hundred plants for every ten he devours; or the well-adapted parasite who, if he could, would be the first to prolong the life of his host?

Ethics aside, parasitism specifically, and symbiosis generally, illustrate most strikingly how very intimately the members of a living community are interdependent.

REVIEW QUESTIONS

- 1. What, specifically, is a population, a society, a community, a symbiotic association? Make sure that you understand the interrelation of these units.
- 2. How do new species arise, and in what general ways are two sister species different?
- 3. What are individual variations? Distinguish between inheritable and noninheritable variations, and give examples of each. What are adaptive variations?
- 4. Review the organization of some insect and vertebrate societies, and contrast these organizations. What is the social significance of family groupings, and where do the latter occur? What is the significance of animal migrations? Of peck orders?
 - 5. Define communal succession, climax community,

food pyramid, mimicry. Review the nutritional, reproductive, and protective links which hold the members of a community together. How are long-range numerical population balances maintained? In what ways are populations, species, and communities specialized?

- 6. What are the various forms of symbiosis, and how are they defined? Give concrete examples of each.
- 7. What is hyperparasitism, ectoparasitism, endoparasitism?
- 8. What general structural and functional characteristics distinguish parasites from free-living organisms? How do parasites transfer from host to host?
- 9. Describe the life cycles of tapeworms, and review the general significance of intermediate hosts.

SUGGESTED COLLATERAL READINGS

- Burnet, F. M.: Viruses, Sci. American, vol. 184, 1951.
- Cleveland, L. R.: An Ideal Partnership, Sci. Monthly, vol. 67, 1948.
- Guhl, A. M.: The Social Order of Chickens, Sci. American, vol. 194, 1956.
- Krough, A.: The Language of Bees, Sci. American, vol. 179, 1948.
- Luria, S. E.: The T2 Mystery, Sci. American, vol. 192, 1955
- Lwoff, A.: The Life Cycle of a Virus, Sci. American, vol. 190, 1954.
- Smith, R. F., and W. W. Allen: Insect Control and the Balance of Nature, Sci. American, vol. 190, 1954.
- Tinbergen, N.: "Social Behavior in Animals," Wiley, 1953.
- Zinsser, H.: "Rats, Lice, and History," Little, Brown, 1935.

CHAPTER 5

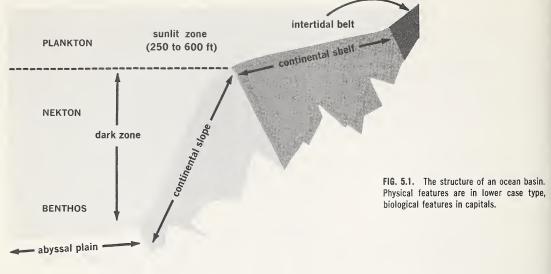
Community and environment

In this chapter, we add the finishing touches to our characterization of the living world. Our scale of view now becomes global, and we examine the living world as a whole.

Different environments harbor different kinds of communities, and an inquiry into the nature of these various communal homes, or habitats, forms our first topic. The second topic deals with the physical, chemical, and geological forces which affect the habitats and the organisms in them and which actually govern environmental conditions on the entire earth. In other words, we shall examine the large-scale nature of the global environment.

THE COMMUNAL HABITATS

With the possible exception of the most arid deserts, the high frozen mountain peaks, and the perpetually icebound polar regions, probably no place on earth is devoid of life. The large subdivisions of this planetary home are the aquatic and the terrestrial habitats. Both range from equator to pole and from a few thousand feet below to a few thousand feet above sea level. Ocean and fresh water are the principal components of the aquatic habitat, and air and soil of the terrestrial.



The oceanic habitat

The ocean basin. All ocean basins have roughly the form of an inverted hat (Fig. 5.1). A gently sloping continental shelf stretches away from the coast line for an average distance of about 100 miles (discounting often extreme deviations from this average). The angle of descent then changes more or less abruptly, and the shelf grades over into a steep continental slope. Characteristically, this slope is scored deeply by gorges and canyons, carved out by slow rivers of mud and sand discharging from estuaries. Several thousand feet down, the continental slope levels off into the ocean floor, a more or less horizontal expanse known as the abyssal plain. Mountains rise from it in places, with peaks sometimes so high that they rear up above sea level as islands. Elsewhere, the plain may be scarred by deep rifts, e.g., the deeps just east of the Philippines and Japan which, plunging 35,000 ft down, are the lowest parts of the earth's crust.

Each subdivision of the "wall" of such a basin represents a distinct subenvironment of the ocean

and is inhabited by specially adapted communities of organisms. Moreover, the water itself which fills the basin is subdivided by the sun into two major subenvironments. Acting directly or via the overlying medium of air, the sun produces "weather" in the surface layers of the sea-waves, current, storm, evaporation, seasons, daily climatic rhythms, and other changes. Deep water is not so affected. Moreover, sunlight penetrates into water only to an average depth of about 250 ft and to at most 600 ft in certain seas. Below this sunlit top layer, the ocean is eternally and completely dark. The most significant consequence of this is that photosynthesizing vegetation can exist only in the uppermost layers of the sea. Animal life directly dependent on plant foods therefore must remain near the surface too. As a result, the top 250 ft or so of the oceans contains a concentration of living matter as dense as any on earth.

On the basis of its relationship to these various environments, marine life has been classified into three general categories: plankton, nekton, and benthos. Plankton includes all passively drifting or floating forms. Most of them are microscopic and are found largely in the sunlit surface waters of the sea. Even though some of them possess locomotor systems, they are nevertheless too weak or too small to counteract currents and movements of water. Nekton comprises the active swimmers, capable of changing stations at will. Nektonic types are therefore found in all waters, along the surface as well as in the sea depths. And the benthos consists of crawling, creeping, and sessile organisms along the walls and floor of the sea basin.

The surface waters. The predominant marine flora in the sunlit layers is planktonic. It consists of teeming trillions of algae, which as a group, probably photosynthesize more food than all other photosynthesizing organisms combined. This marine vegetation represents the richest pasture on earth; directly or indirectly, it forms the nutritional basis of all marine life.

Most of the algal types included in this "grass of the sea" are microscopic, and they remain afloat by buoyancy. Unquestionably the most abundant are the diatoms. Each of these single-celled algae is enclosed within a delicate, intricately sculptured, silicon-containing shell (Fig. 5.2). Reddish algal dinoflagellates also abound in surface waters, sometimes in populations so dense that they tint acre upon acre of ocean with a coppery hue (e.g., "red" tides). Other marine algae include many types of variously pigmented forms, and some of these, as well as countless numbers of marine bacteria, are bioluminescent. They emit flashes of cold light, which dot the night seascape with a billion pin points of greenish fire.

In certain circumscribed regions (e.g., the Sargasso Sea in the mid-Atlantic) are also present larger, multicellular algae—flat, sheetlike seaweeds, often equipped with specialized air bladders which aid in keeping the organisms afloat. Such seaweeds may sometimes aggregate in considerable numbers over wide areas, particularly if a region is ringed in by ocean currents and therefore remains relatively isolated and stagnant.

Living side by side with the plankton flora in the surface waters is the plankton fauna: protozoa, eggs,

larvae, tiny shrimp, and countless other small animals carried along by surface drift. They feed directly on the microscopic vegetation. A good part of the nekton, largely fishes and marine mammals, lives in these surface waters too, feeding either on the plankton or on one another.

Nearer to shore, in the waters above the continental shelf, even a bottom dweller is likely to be within the range of sunlight. The problem therefore is not so much to remain affoat as to remain attached to solid ground, for close to shore the force of waves and of ground swells is considerable. And in the tide zone, an even more profound problem is the ebbing of water twice daily and the consequent rhythmic alternation between aquatic and essentially terrestrial conditions. Also, in waters in and for miles beyond estuaries, fresh water discharging from rivers mixes with ocean water, a circumstance introducing additional environmental inconstancies. Being the meeting ground of water, land, and air, the tide zone is actually among the most violently changing environments on earth.

Vegetation in these coastal waters is again largely algal. In addition to the planktonic types, attached forms abound. Most of these are equipped with specialized holdfasts which anchor the algae to underlying ground. The animals in this region include numerous planktonic forms, nektonic forms (largely fish), and an abundance of sessile and creeping types which are variously adapted to rocky, muddy, or sandy bottoms. These animals make use of all conceivable dwelling sites: tide pools left on rock by ebbing water, crevices and hollows in and under rock, burrows in sand or mud, the sheltered water among vegetation and among sessile animal growths, empty shells and other skeletons of dead animals, and flotsam and jetsam along the shore and in deeper water.

The deep waters. The contrast between the surface environments within reach of the sun and those underneath is dramatic. As the former are forever fluctuating, so are the latter perennially steady and relatively unchanging. The deep ocean is still little explored, and for many this "last frontier" has

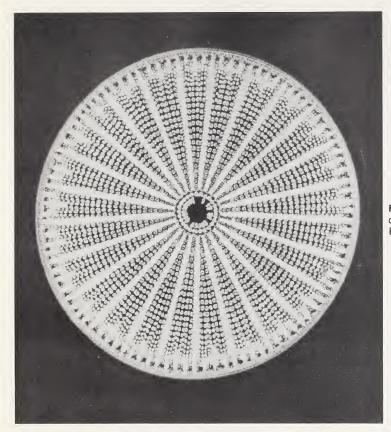


Fig. 5.2. The finely sculptured silicon shell of a diatom. See also Fig. 7.9. (General Biological Supply House, Inc.)

acquired a romance and mystery all its own. Several unique physical conditions characterize this world of the sea depths.

First, the region is one of eternal night. In the total absence of sunlight, the waters are pervaded with a perpetual blackness of a kind found nowhere else on earth.

Second, seasons and changing weather are practically absent. Localized climatic changes do occur,

as a result of occasional submarine volcanic activity or, more regularly, through deep-sea currents. These produce large-scale shifts of water masses and, incidentally, bring oxygen to even the deepest parts of the ocean. Being beyond the influence of the sun, the deep waters are cold, unchangingly so. The temperature is about 1°C along the sea floor.

Third, water pressure increases steadily from the surface down, 1 atmosphere (atm) for every 33 ft of

descent. Thus in the deepest trenches of the ocean, the pressure is about a thousand times as great as at sea level.

And fourth, a continuous slow rain of the dead remnants of surface organisms drifts down toward the sea bottom. Much of this material, particularly the organic fraction, dissolves completely during the descent. But much microscopic mineral matter reaches the abyssal plain, where it forms everthickening layers of ooze. Accumulating over the millennia, the older layers eventually compress into rock. Vertical-bore samples of such rock have revealed a great deal of the past history of the oceans and their once living surface inhabitants.

Contrary to early beliefs that life should be impossible in such an environment, a surprisingly rich diversity of organisms has been found to exist practically everywhere in the free water and along the floor of the deep sea. The community is uniquely and exclusively animal; photosynthesizing plants are confined to the sunlit surface. Virtually all animals are represented, many by—to us—strange and bizarre types uniquely adapted to the locale (Fig. 5.3).

Because there are only animals present (apart from bacteria), the deep sea is the most competitive environment on earth. The very structure of the animals underscores their violently carnivorous, "eat-or-be-eaten" mode of existence. For example, most of the fishes have enormous mouths equipped with long, razor-sharp teeth, and many can swallow fish larger than themselves.

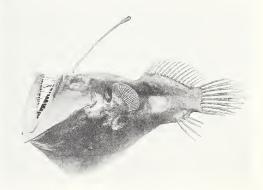
Since the environment is pitch-black, one of the critical problems for these animals is to find food to

FIG. 5.3. Deep-sea fishes. Three kinds of oceanic angler fishes are shown. The animal in (a) is a female. The structure above the eye is a parasitic male, which is carried about permanently attached. This neatly solves the problem of finding mating partners in the dark. The "beard" of the animal in (b) is probably luminescent. Many of these large-mouthed, dagger-toothed fishes are surprisingly small. For example, the animal in (c) would fit comfortably into the palm of a human hand. (American Museum of Natural History.)



(a)





(c)

begin with. A highly developed pressure sense provides one solution. Turbulence in the water created by nearby animals can be recognized and, depending on the nature of the turbulence, may be acted upon either by flight or by approach.

Another important adaptation to the dark is bioluminescence. Many of the deep-sea animals possess light-producing organs on the body surface, of different shapes, sizes, and distributions in different species. The light patterns emitted may include a variety of colors and probably serve partly in species recognition. Identification of a suitable mate, for example, must be a serious problem in an environment where everything appears equally black. Another function of the light undoubtedly is to warn or to lure. Some of the bioluminescent lures have evolved to a high degree of perfection. Certain fish, for example, carry a "lantern" on a stalk protruding from the snout (Fig. 5.3). An inquisitive animal attracted to the light of the lantern will discover too late that it has headed straight into powerful jaws.

The fresh-water habitat

Physically and biologically, the link between ocean and land is the fresh water. Rivers and lakes were the original invasion routes over which some of the descendants of ancestral marine organisms reached land and, in the process, evolved into terrestrial forms. Certain of the migrant types never completed the transition but settled along the way.

Among these, some adapted to the brackish water in estuaries and river mouths, or to a life spent partly in the ocean, partly in fresh water. Very many types could leave the ocean entirely and adapt to an exclusively fresh-water existence. The descendants of this large group include bacteria, algae, and representatives of most major animal types. Some of the ancestral fresh-water organisms later managed to gain a foothold on land, but they still had to spend part of their lives in or near fresh water. Frogs and other amphibia, for instance, are among their modern descendants. Thus organisms which inhabit fresh water for part or all of their lives constitute a major subdivision of the biological world.

Three main conditions distinguish the fresh-water environment from that of the ocean. First, the salt content is substantially lower. In an organism which has evolved, and still lives, in the sea, the internal salt concentration of protoplasm matches that of the marine environment. If such an organism moves to fresh water, the external salt concentrations will be much lower than the internal. For reasons to be explained in the next chapter, the result of this is that water will be pulled from the environment, through the body surface, into the organism. The amount of water in protoplasm will therefore tend to increase, and protoplasm will tend to become diluted.

Fresh-water organisms evidently require, and they actually possess, efficient bailing devices to eliminate the water they continuously ship. Excretory systems, and also digestive systems and gills, serve in this water-balancing function. In animals inhabiting estuaries, where external salt concentrations fluctuate almost continuously, and in organisms whose life cycle includes both marine and fresh-water phases, water- and salt-balancing mechanisms are particularly well developed.

A second general condition characterizing much of the fresh-water environment is the presence of strong, swift currents. Except in large lakes, passively floating life so typical of the ocean surface is therefore not likely to be encountered. On the contrary, the premium will be either on maintaining firm anchorage along the shores and bottoms of rivers or on ability to resist and to overcome the force of currents by muscle power.

Indeed, fresh-water plants are strongly rooted, and fresh-water animals generally are powerful swimmers. The eggs of such animals are enveloped by sticky jelly coats which adhere firmly to plants or other objects in the water. And even the young are strongly muscled from the moment they hatch.

A third major distinction between fresh water and ocean is that the former, with the exception of only the very large lakes, is affected much more by climate and weather than is any part of the latter. Bodies of fresh water often freeze over in winter and may dry up completely in summer. Water temperatures change not only seasonally but also daily, frequently to a considerable extent. Gales or flood conditions may bring bottom mud and silt to the surface and upset the fresh-water habitat in major ways. A large number of factors may alter flow conditions and produce, for example, stagnant water, or significantly altered chemical content, or situations facilitating infectious epidemics. We note that the fresh water shares the environmental inconstancies of the land in very large measure.

The terrestrial habitat

That land environments differ greatly in character is eminently clear to a land dweller as efficient and far-ranging as man. It should also be clear that, regardless of which particular subdivision of the terrestrial environment one considers, the sustaining foundations of all land life are *air* and, directly or indirectly, also *soil*.

Like air, soil is itself a terrestrial home, providing a habitat for a vast array of subsurface organisms. And by creating the conditions necessary for the survival of all other terrestrial organisms, man included, soil becomes a major agency which transforms terrestrial environments into life-sustaining "habitats." Two other agencies play a vital role here: annual temperature and rainfall. As these vary with geographic latitude and altitude, they divide the soil-covered land surface into a number of distinct habitat zones: desert, grassland, rain forest, deciduous forest, taiga, and tundra.

The tropics and subtropics. In the tropics are found representatives of the first three of the six habitats just named. They are characterized here by comparatively high annual temperatures and by daily temperature variations which are greater than the seasonal variations. Differences in the amount of precipitation largely account for the different nature of these habitats.

A desert usually has less than 10 in. of rain per year, concentrated largely in a few heavy cloud-bursts. Desert life is well adapted to this. Plants,

for example, grow, bloom, are fertilized, and produce seeds, all within a matter of days after a rain. Since the growing season is thus greatly restricted, such plants stay relatively small. Leaf surfaces are often reduced to spines and thorns, minimizing water loss by evaporation (see also Chap. 8). Desert animals too are generally small, and they include many burrowing forms which may escape the direct rays of the sun under the ground surface.

Grassland, as everyone well knows, is not an exclusively tropical habitat but extends into much of the temperate zone as well. The more or less synonymous terms "prairie," "pampas," "steppe," "puszta," and many other regional designations underscore the wide distribution of this habitat. The common feature of all grasslands is intermittent, erratic rainfall, amounting to about 10 to 40 in. annually. Grassland probably supports more species of animals than any other terrestrial habitat. Different kinds of mammals are particularly conspicuous.

In those tropical and subtropical regions in which torrential rains fall practically every day and where a well-defined rainy season characterizes the winter, plant growth continues the year round. Lush rain forests have developed here (Fig. 5.4), typified particularly by the communal coexistence of up to several hundred different species of trees. Rain forests are the "jungles" of the adventure tale. They cover much of central Africa, south and southeast Asia, Central America, and the Amazon Basin of South America. Trees in such forests are normally so crowded together that they form a continuous overhead canopy of branches and foliage, which cuts off practically all the sunlight, much of the rain water, and a good deal of the wind. As a result, the forest floor is exceedingly humid and quite dark and it is populated by plants requiring only a minimum of light. Animal communities too are stratified vertically, according to the several very different habitats offered between canopy and ground. The tropical rain forest is singularly quiet during the day, but it erupts into a cacophony of sound at night, when the largely nocturnal fauna becomes active.



FIG. 5.4. (a) The habitat of the rain forest. Many dozens of different plant types, coexisting in dense formations, are generally characteristic of it. (b) A subtropical palm forest. The trees of such forests may retain their foliage the year round. [(a) National Park Service; (b) U.S. Forest Service.]

The temperate and polar regions. In the temperate zone, apart from extensive grasslands and occasional deserts, the most characteristic habitat is the deciduous forest. The fundamental climatic conditions here are cold winters, warm summers,



and well-spaced rains bringing some 30 to 40 in. of precipitation per year. The habitat is characterized also by seasonal temperature variations which are greater than the daily variations. Winter makes the growing season discontinuous, and the flora is adapted to this. Trees are largely *deciduous*, that is, they shed their leaves in late fall; and small annual plants produce seeds which withstand the cold weather. A deciduous forest differs from a rain forest in that trees are spaced farther apart and in that far fewer species are present. Compared with the hundreds of tree types in the one, there may be only some 10 or 20 in the other.

North of the deciduous forests and the grasslands, across Canada, northern Europe, and Siberia, stretches the taiga (Fig. 5.5). This is a habitat of long severe winters and of growing seasons limited largely to the few months of summer. Hardy conifers, spruce in particular, are most representative of the flora, and moose, wolves, and bears, of the fauna. The taiga is preeminently a zone of forests. These differ from other types of forests in that they usually consist of a single species of tree. Thus,



FIG. 5.5. The habitat of the taiga. Note the predominance of a single species of tree over large areas, characteristic of the taiga generally. (National Park Service.)

over a large area, spruce, for example, may be the only kind of tree present. Another conifer species might be found in an adjacent, equally large area. Occasional stands of hardy deciduous trees are often intermingled with conifers. An accident of geography makes the taiga a habitat characteristic of the Northern Hemisphere only: little land exists in corresponding latitudes of the Southern Hemisphere.

The same circumstance makes the tundra, most polar of terrestrial habitats, a predominantly northern phenomenon (Fig. 5.6). Much of the tundra lies within the Arctic Circle. Hence its climate is cold and there may be continuous night during the winter season and continuous daylight, of comparatively low intensity, during the summer. Some distance below the surface, the ground is permanently frozen, and aboveground, frost can form even during the summer—plants often freeze solid and remain dormant until they thaw out again. The growing season is very brief, as in the desert, but in the tundra the limiting factor is temperature, not water supply. Plants are low, ground-hugging

forms, and trees are absent. Lichens, mosses, coniferous and other shrubby growths, and herbs with brilliantly colored flowers, all blooming simultaneously during the growing season, are characteristic of the habitat. Conspicuous among the animals are hordes of insects, particularly flies, and a considerable variety of mammals: caribou, arctic hares, lemmings, foxes, musk oxen, and polar bears. Birds are largely migratory, leaving for more southern latitudes with the coming of winter.

Life does not end at the northern margin of the tundra, but extends farther into the ice and bleak rock of the soilless polar region. Polar life is almost exclusively animal. And it is not really terrestrial anyway, but is based on the sea (e.g., walruses, seals, penguins).

We may note that the horizontal sequence of habitats between equator and pole is repeated more or less exactly in a vertical direction, along the slopes of mountains (Fig. 5.7). Thus habitat zones which are spread over thousands of miles latitudinally are telescoped altitudinally into a few thousand feet.



FIG. 5.6. The habitat of the tundra. Note complete absence of trees in both views. (Courtesy of U. C. Nelson and H. C. Oberholser, U.S. Fish and Wildlife Service.)

The foregoing should make it clear that the nature of any kind of habitat, hence the nature of its living communities, is determined by a few persistently recurring variables. Among them are solar light, solar heat, geographic latitude, vertical depth and altitude, rainfall, wind and water currents, and the chemical composition of the locale. Variables like these are of global importance, and together they add up to the large-scale "environment."

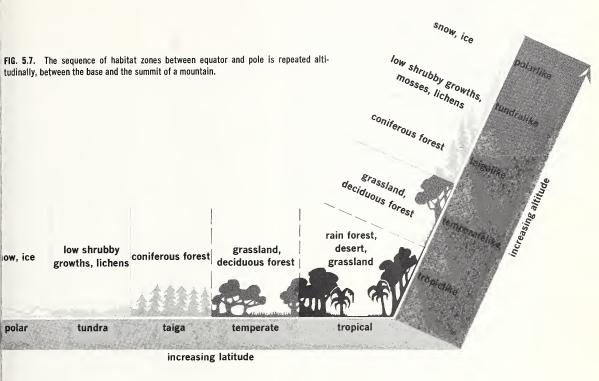
With this we reach the highest organizational level on earth: the earth itself as a unit, with its integrated living and nonliving components.

THE GLOBAL ENVIRONMENT

The most important single observation we can make about the earthly environment as a whole is that it is forever changing, on every scale from the submicroscopic to the global. As a direct consequence, living matter too must constantly change: it must adjust internally if it is to maintain steady states; it must reproduce if it is to offset environmental destruction; and it must evolve if it is to stay adapted to its surroundings. As we have seen, the very origin of living matter was itself a result of environmental change, and protoplasm subsequently became a powerful cause of continued change.

What, fundamentally, produces this constant change? The earth as a whole, hence protoplasm and every other subordinate part, is an open system: a system which exchanges materials and/or energy with its surroundings. Not much material enters or leaves the earth, but energy both enters and leaves. A broad spectrum of solar energy, from heat rays to X rays, beams in all the time, and an enormous amount of energy radiates away, principally in the form of heat. As a result, the earth's material substance can never attain static equilibrium. For so long as the sun shines and the earth spins, energy change will create balance-upsetting disturbances. Every imbalance creates new imbalances of its own, and as a general consequence, the earth's environment is forever changing.

These changes occur predominantly in rhythmic cycles. Daily and seasonal climatic cycles are familiar examples. Other environmental cycles may be less readily discernible, particularly if their scale is too vast or too minute or if they occur too fast or too slowly for direct observation. The three categories of environmental cycles are the geophysical, the geochemical, and the biological. The last, which includes population cycles within communities and cycles of communal succession, in effect have already been dealt with earlier. Here, therefore, we shall discuss only the first two types and, in particular.



their interrelation with the biological component of the environment.

Geophysical cycles

These cycles include, principally, climatic and geological changes, produced partly by solar and other astrophysical causes, partly by events on and within the earth itself.

Climatic change. A discussion of climate ultimately becomes a discussion of water and of the temperature changes to which water is subjected. For the earth is a world of water. The most widely distributed and most abundant mineral on the

planet, water covers 73 per cent of the earth's surface entirely, and it is present in the atmosphere, in rocks, indeed in virtually all objects and all regions.

The world's waters play a principal part in the following climatic cycles:

- 1. **Evaporation** of warmed water produces humidity and clouds. Subsequent rain and snow form rivers, which replenish the ocean.
- 2. Ocean water warmed in the tropics becomes light and rises to the surface, whereas cool polar water sinks. These up-down displacements bring about massive horizontal shifts of water between equator and pole. The rotation of the earth introduces east-west displacements, and these effects,

reinforced substantially by similarly patterned wind- and wave-producing air movements, result in oceanic currents. These influence climatic conditions not only within the seas, but also in the air and on land.

- 3. Of all liquids, water is one of the slowest to heat or cool, and it stores a very large amount of heat energy. The oceans thus become huge reservoirs of solar heat. The result is that sea air chilled by night, or in winter, becomes less cold because of heat radiation from water warmed by day, or in summer; and that sea air warmed by day, or in summer, becomes less hot because of heat absorption by water cooled by night, or in winter. Warm or cool onshore winds then moderate the inland climate in daily and seasonal patterns.
- 4. Over long periods of time, global climatic conditions are determined by the relative amount of water locked into polar ice. Temperature variations averaging only a few degrees over the years, produced by still poorly understood geophysical changes, suffice for major advance or retreat of polar ice. During the last million years, "ice ages" have developed and waned rhythmically and warm interglacial periods, characterized by ice-free poles, have intervened between successive advances of ice. Four glaciation cycles have occurred, each lasting in the order of 60,000 to 200,000 years. At the present time, the earth is slowly emerging from the last ice age, which reached its peak some 50,000 to 20,000 years ago (Chap. 24). As polar ice is melting, water levels are now rising and coast lines are gradually being submerged. If trends during the past fifty years are reliable indications, the earth appears to be warming up generally. Deserts are presently expanding; snow lines on mountains are receding to higher altitudes; in given localities, more days of the year are snow-free; and the flora and fauna native to given latitudes are slowly spreading poleward. It is difficult to be sure whether these changes are merely part of a short warm cycle or are really indicative of a long-range trend.

Directly or indirectly, these and other climatic cycles materially affect living matter; organisms are

largely water, and protoplasmic water is influenced by the weather just as any other kind. Even man, who like other mammals and birds possesses an internal temperature- and evaporation-regulating mechanism, feels the effect of climate in all parts of the body, as everyone well knows.

In some instances, living matter in turn affects climate. For example, the trees of tropical jungles release so much water vapor that the air over vast areas remains permanently saturated with moisture. Significant on an even larger scale is the release of carbon dioxide by living creatures and by the industrial installations of modern man. As this gas accumulates, it adds to the heat-retaining potential of the atmosphere. Over the millennia, therefore, CO₂ may contribute to the development of warmer climates all over the globe.

Geological change. Geological cycles generally span thousands and millions of years, and their effects on living organisms are often so profound that the only adequate response is rapid evolution.

One of the most important cycles here involves the rising and lowering of land. Major parts of continents, or indeed whole continents, may be lifted higher when the land is pushed up from below or is pressed from the sides by adjacent portions of the earth crust. To be sure, changes of this sort take place exceedingly slowly. They are counteracted, equally slowly, by leveling of high land through erosion.

The most dramatic instance of such cycles is mountain building and mountain leveling. Presently the youngest, hence the highest, mountain ranges are the Himalayas, the Rockies, the Andes, and the Alps. All of them were thrown up some seventy million years ago, and we may note that the earth's crust in these regions is not completely settled even now.

Quite apart from the tremendous upheaval caused by mountain formation itself, such an event has long-lasting climatic consequences. A high, massive mountain barrier is likely to interfere drastically with continental air circulation. For example,

moisture-laden ocean winds may no longer be able to pass across the barrier. Continual rain will therefore fall on the near side, and the region may become lush and fertile. By contrast, the far side will be arid, and desert conditions are likely to develop (Fig. 5.8). Two good examples: fertile California on the ocean side of the Rockies and the deserts of Arizona and New Mexico on the other: fertile India on the ocean side of the Himalayas and the belt of deserts north of them. Plants and animals living on either side of a newly formed mountain range must adapt to the new environmental conditions by evolution. As we shall see, periods of extensive mountain building have always been followed by major evolutionary turnover among organisms (Chap. 24).

In time, even the highest mountains wear away, principally through the erosive action of water. Thus water and gravity produce shearing, canyon-cutting rivers (Fig. 5.9). Water and low temperatures produce grinding, rock-pulverizing glaciers, and as freezing water expands in rocky crevices, it carves boulders and stones off the face of a mountain. Water and high temperatures produce corrosive humidity, and water dissolves rock by chemical action. Water, wind, and sun in time thus reduce mountain to hill, and hill eventually to plain.

Interplay between land and sea produces other geological cycles. Land is eroded away as wind-whipped waves batter the shore, topple cliffs, crumble stone, and wash out beaches. But new land appears where rivers deposit silt and where tongues of land or growing sand bars cut off shallow, slowly evaporating arms of the sea.

Another land-sea cycle is brought about by the alternate growth and recession of polar ice. With the fluctuation of ice, the sea level falls or rises; hence coastal lands around the globe enlarge or disappear. Also, narrow bridges of land may emerge or submerge and the outline of continents may change. Note here that the lifting of land too may bring about a change in the contours of the continents.

In still another cycle, submarine volcanic action

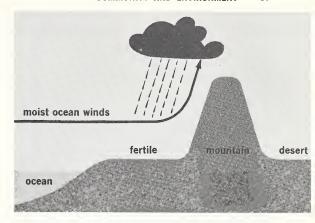


FIG. 5.8. The effect of a mountain on climate. A mountain deflects moisture-rich ocean winds upward and causes rain to remain confined to the slope facing the ocean. That slope will therefore be fertile, but the far slope will become a desert.

may thrust up new oceanic islands and existing islands may become submerged. Living matter itself on occasion contributes to the growth of new land. For example, coral islands and atolls are the products of countless sessile coelenterates, which extract calcium salts from the sea and build their skeletons from them. When the animals die, their offspring build onto the skeletons of their forebears. On an even larger scale, myriads of tiny marine surface organisms die every second, and as noted earlier, their microscopic skeletal shells rain down to the sea floor. There they accumulate layer by layer for millions of years, building up here and there into thick rocky crusts. These may eventually be exposed as new land.

The many components of unending geophysical change thus include temperature, pressure, gravitation, radiation, evaporation, ice, humidity, wind, waves, dissolution, corrosion, erosion, and the heaving of the earth crust. Living matter must cope with all these geophysical changes or die. Moreover, living matter must also cope with geochemical change.



FIG. 5.9. The cutting, erosional effect of a river. This canyon was channeled out by the stream flowing through it. (U.S. Department of Agriculture.)

Geochemical cycles

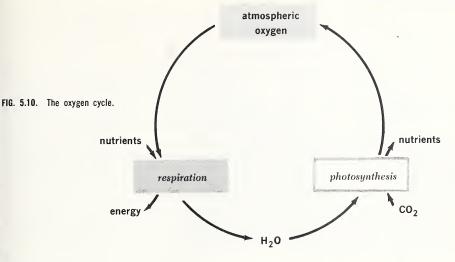
Partly because of geophysical change, partly because of the metabolic activity of living organisms, all chemical constituents of the earth's surface circulate in vast cycles. Protoplasm is an important component in these. The entire substance of living matter is composed of materials drawn ultimately from the physical surroundings, and after a temporary stay in protoplasm, all these materials return to the earth, often to contribute again to new living matter. On a finite planet, such conservation of materials is a fundamental requirement for long-continued perpetuation of life.

Water. The basic cycle is the sea-air-land-sea circulation which, as described above, is maintained by evaporation and precipitation. Living organisms are interposed at all points: sea, air, and land, all contribute water to protoplasm. Such water is turned over fairly quickly, much of it is soon returned to sea, air, or land by excretion and evaporation. A relatively constant amount is retained within protoplasm until death, when that quantity too passes back into the environment.

Atmospheric gases. The present atmosphere consists mainly of oxygen (O_2) , about 20 per cent; carbon dioxide (CO_2) , about 0.03 per cent; nitrogen (N_2) , about 79 per cent; water in varying amounts, depending on climatic conditions; and minute traces of inert gases (helium, neon, krypton, argon, xenon). Excepting the inert gases, all these components of air are vital protoplasmic raw materials, and they are drawn either directly from the air or from natural waters in which they are dissolved.

Atmospheric oxygen enters living organisms as a respiratory gas, and it eventually passes back to the environment or, in combination with hydrogen, forms water. This water is a byproduct of respiration, and we shall see how it is produced within organisms, in Chap. 13. The water may then be used as a raw material in photosynthesis, in which process the oxygen part of the water is again liberated. This O₂ byproduct then passes back to the atmosphere, thereby completing the cycle (Fig. 5.10).

Atmospheric carbon dioxide is the carbon source of protoplasm. This gas enters the living world through photosynthesis, in which it is a fundamental raw material. Photosynthesis converts CO₂ into foods, and these then serve living organisms in

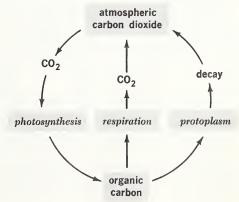


two ways. Some of the foods are used in respiration, which returns CO_2 to the environment as a byproduct. The remaining foods become part of the protoplasm of organisms. After death, protoplasm decays by bacterial action and CO_2 is released in the process (Fig. 5.11). Note that the CO_2 content of air also increases through combustion of industrial fuels, through forest and other fires, and to some extent also through occasional additions from the interior of the earth (e.g., volcanic eruptions).

Atmospheric N₂ is the principal nitrogen source for living organisms. However, molecular nitrogen (N₂) is rather inert chemically and the majority of organisms actually cannot use it directly. For example, man obtains an abundance of aerial nitrogen with every breath, yet all of it is again exhaled, unchanged and unused. The situation is essentially similar in most other organisms. Only certain bacteria, the so-called nitrogen-fixing bacteria, may utilize atmospheric N₂ directly, and they manufacture nitrates out of it. Nitrates (NO₃⁻) are chemicals which accumulate in soil or ocean (and sometimes man enriches the soil by adding nitrate fertilizers). From this source nitrates are absorbed by plants as

mineral nutrients. Plants in turn can change nitrates chemically into usable forms of nitrogen (e.g., amino groups, —NH₂), which can become part of plant protoplasm. Animals then depend on plant foods for their own source of usable nitrogen. After plants and animals die they decay, and as a result

FIG. 5.11. The carbon cycle.



the nitrogen of their bodies appears in soil or ocean as ammonia (NH_3). This substance is subsequently acted on by two specialized types of bacteria. The nitrifying bacteria convert NH_3 back to nitrates (NO_3 -), and so they reenrich the nitrate supply of the environment. And the denitrifying bacteria change ammonia back into atmospheric nitrogen, N_2 , thereby completing the cycle (Fig. 5.12).

Mineral solids. Turnover of the solid components of the earth's surface is correlated with the geological cycles discussed above. Rock and sand are slowly eroded by water, and most of the constituents of stone thereby become dissolved minerals and salts. These inorganic substances are carried by rain into rivers and soil, where they may be used as nutrients by living organisms. After the organisms die, their inorganic components return to river and soil. This completes a continental mineral cycle.

Soil minerals leach into rivers, and rivers drain into the ocean. Hence as the land is slowly being denuded of mineral compounds, the seas fill with them. Another cycle now exists in the ocean: marine flora and fauna incorporate required minerals into their protoplasm, and upon death these minerals are reclaimed by the sea.

Completion of the global mineral cycle involves the settling of bones, shells, and other mineral precipitates on the ocean floor and subsequent upthrusting of the sea bottom, or the dropping of sea level, exposing new land (Fig. 5.13).

We have completed our characterization of the living world. From atom through molecule, nucleo-protein, cell, organism, species, community, to the whole environment, the ever-recurring theme has been progressive aggregation; the ever-recurring result, progressive interdependence, cooperation, specialization, and greater economy and efficiency in maintaining and perpetuating life.

The aggregative process has not yet entirely saturated the living hierarchy. Thus the social level exists, but it is rare, and in our own case it is certainly not startlingly perfected as yet. Room for

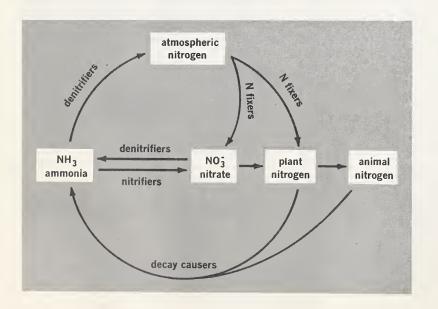
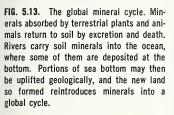
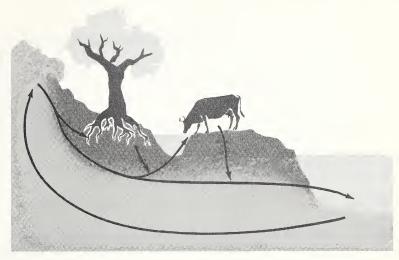


FIG. 5.12. The nitrogen cycle.





organizational improvement is actually ample at all levels. Moreover, origination of altogether new levels, interpolated between existing ones, is also well within the bounds of possibility. The modern drawing together of mankind into ever-larger aggregates of nations may be just such an interpolation. If so, the net result of such aggregative processes should be predictable: more efficient, cooperative survival, at the expense of some of the independence of subordinated units.

REVIEW QUESTIONS

- 1. What is the structure of an ocean basin? What are the major subenvironments in such a basin, and what role does the sun play in creating some of these subenvironments? What physical conditions characterize the various subenvironments?
- **2.** Define plankton, nekton, and benthos. Give specific examples of each. Where in the ocean are each of these types of organisms found?
- 3. What physical and biological conditions characterize the sea depths?
- 4. Review the essential physical differences between oceanic and fresh-water environments. What major types of organisms occur in fresh water, and in what general ways are they adapted to this environment? What major types of organisms are terrestrial?
 - 5. What are the main terrestrial habitats, and what

- physical and biological conditions characterize each of these? In what way are latitudinal terrestrial habitats related to altitudinal habitats?
- 6. Why is the global environment always changing and never stable? What are the main categories of ways in which the global environment is changing?
- 7. How do the world's waters influence climates? How does the formation of mountains influence climates? Cite examples.
- 8. Review some of the major geological cycles which produce environmental change. What role does water play in geological cycles?
- **9.** Review the global water, oxygen, carbon dioxide, and nitrogen cycles. How does man obtain his nitrogen supply?

SUGGESTED COLLATERAL READINGS

- Carson, R.: "The Sea Around Us," Oxford, 1951.
- Cole, L. C.: The Ecosphere, Sci. American, vol. 198, 1958.
- Deevey, E. S.: Life in the Depths of a Pond, Sci. American, vol. 185, 1951.
- Kamen, M. D.: Discoveries in Nitrogen Fixation, Sci. American, vol. 188, 1953.
- Kimble, G. H. T.: The Changing Climate, Sci. American, vol. 182, 1950.
- Nicholas, G.: Life in Caves, Sci. American, vol. 192, 1955. Ryther, F. H.: The Sargasso Sea, Sci. American, vol. 194, 1956.
- Vevers, H. G.: Animals of the Bottom, Sci. American, vol. 187, 1952.
- Walford, L. A.: The Deep-sea Layers of Life, Sci. American, vol. 185, 1951.
- Went, F. W.: The Ecology of Desert Plants, Sci. American, vol. 192, 1955.

Part Two

THE LIVING ORGANIZATION

The preceding sequence of chapters was a characterization of the living world as a whole. The present sequence begins a more detailed characterization of living structures and functions.

We have found that living matter, protoplasm, is structured by levels and that we regard it as living because it carries out the functions of metabolism and self-perpetuation. Our first objective in this series of chapters is to take a closer look at protoplasm and to examine in greater detail its composition, its properties, and its organization into **cells**.

Cells in their turn make up the organisms of the living world. Accordingly, our subsequent objective in this series will be to study the diverse kinds of whole **plants** and **animals** made up out of cells, their internal organization, and the diverse ways of life which these organisms pursue.

The following four chapters deal with these topics. They also serve to set the stage for a later examination of protoplasmic functions.

CHAPTER 6

Protoplasm and cells

Regardless of where, when, or how we examine the structure of any bit of protoplasm, we ultimately find it to consist entirely of *chemicals*—atoms and molecules. And regardless of what particular function of protoplasm we examine, that function is ultimately always based on the properties of the atomic and molecular components.

In this chapter, therefore, we first identify the main types of atoms and molecules of which protoplasm is composed. Actually we have already discussed this briefly in Chap. 2, but a systematic review at this stage is desirable. Next, we examine some of the main properties which protoplasm dis-

plays by virtue of being made up of a given collection of chemicals. And finally, we deal with the ways in which protoplasm is organized into biological units, the basic unit here being the cell.

THE COMPOSITION OF PROTOPLASM

Four of the most widely distributed chemical elements on earth make up approximately 95 per cent of the weight of protoplasm: oxygen, 62 per cent; carbon, 20 per cent; hydrogen, 10 per cent; and nitrogen, 3 per cent. About 30 other elements contribute the remaining 5 per cent of the weight.

Those listed in Table 3 occur in virtually all types of protoplasm. Trace amounts of others are found only in particular types, and still other elements may become incorporated into living matter accidentally, along with food. All these elements, we recall, are present in the ocean; having originated in water, protoplasm reflects the composition and content of water.

TABLE 3. The relative abundance of chemical elements in living matter

Element	Symbol	Weight per cent
Oxygen	0	62
Carbon	C	20
Hydrogen	H	10
Nitrogen	N	3
Calcium	Ca	2.50
Phosphorus	P	1.14
Chlorine	Cl	0.16
Sulfur	S	0.14
Potassium	K	0.11
Sodium	Na	0.10
Magnesium	Mg	0.07
Iodine	I	0.014
Iron	Fe	0.010
		99.244
Trace elements		0.756
	+	100.00

Virtually all the elements occur in the form of compounds. As already noted in Chap. 2, protoplasm consists of two great classes of compounds: inorganic compounds, i.e., those of mineral nature, and organic compounds, i.e., those which contain linked carbon atoms.

The inorganic components

Directly or indirectly, all inorganic compounds of living matter are of mineral origin; that is, they are supplied in finished form by the external physical environment. Water is the most abundant protoplasmic mineral, present in amounts ranging from 5 to 90 or more per cent. For example, the water content of tooth enamel and of certain plant seeds

is 5 per cent; of marrowless bone, 25 per cent; of whole bone, 40 per cent; of muscle, 75 per cent; of brain, 80 per cent; of milk, 90 per cent; of a jellyfish, at least 90 per cent. A human being is about 67 per cent water, overall, which is a general average for protoplasm as a whole (Fig. 6.1).

Mineral solids make up the other inorganic components of protoplasm. They are present in amounts ranging from 1 to about 5 per cent, on an average. A considerable fraction of the minerals may exist in the form of hard bulk deposits, such as bone, teeth, or shells. These are often silicon- or calcium-containing substances. Other protoplasmic minerals are in solution, either free or combined with organic molecules.

Some of the main chemical elements which make up the mineral solids are listed in Table 3. We shall later encounter a number of molecules, composed of some of these elements, which form specific mineral solids of protoplasm. Here we may note generally that protoplasmic minerals also are major constituents of the ocean and of rocks and ores. Rocks are dissolved by water, water finds its way into the ocean and into soil, and living matter draws its mineral supplies from these sources.

The organic components

Protoplasm contains hundreds of different categories of organic constituents, all distinguished by containing linked carbon atoms. Most of these categories we shall not have occasion to refer to at all. Some we shall encounter in special contexts. And a few will demand most of our attention. In abundance and importance, these few form the organic basis of protoplasm, and they are found in all types of living matter. We have already identified them in Chap. 2: carbohydrates, fats, proteins, and nucleoproteins.

Like mineral compounds, some of these organic substances may contribute to the formation of protoplasmic hard parts. For example, wood, horn, and *chitin*, the external covering of insects and of many other organisms, are predominantly organic. More generally, however, organic materials are dissolved

or suspended in water. Their relative abundance varies considerably in different types of protoplasm. In man, proteins make up about 15 per cent of the total weight, fats about 13 per cent, and all other organic constituents together do not exceed about 1 per cent (Fig. 6.1).

Carbohydrates. Carbohydrates are so called because they consist of carbon, hydrogen, and oxygen, the last two in a 2:1 ratio, as in water. Sugars are the principal carbohydrates, and glucose (C₆H₁₂O₆) is probably the most important of the protoplasmic sugars.

As noted in Chap. 2, it is a general characteristic of organic compounds that even slightly different arrangements of atoms give different kinds of molecules. In glucose, the H and O atoms are joined to a chain of six carbons in a particular pattern:

If the H's and O's are rearranged, the resulting molecule still has the overall atomic formula $C_6H_{12}O_6$ but its properties have become different. The new molecule is, in fact, a different sugar. Depending on how the H and OH groups of glucose are rearranged, the resulting new sugar might be fructose, fruit sugar, or galactose, present in milk, or one of a number of other six-carbon sugars found in protoplasm, all with the atomic formula $C_6H_{12}O_6$.

Under appropriate conditions, sugars may combine with one another. For example, one molecule of glucose can join another like molecule, giving a new 12-carbon sugar, maltose, or malt sugar. One

molecule of water forms as a byproduct in this reaction:

$$\begin{aligned} \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 + \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 &\to \mathbf{C}_{12}\mathbf{H}_{22}\mathbf{O}_{11} + \mathbf{H}_2\mathbf{O} \\ \text{glucose} & \text{glucose} & \text{maltose} \end{aligned}$$

Or glucose can combine with fructose, resulting in the familiar sucrose, cane sugar or beet sugar, used daily by practically everyone:

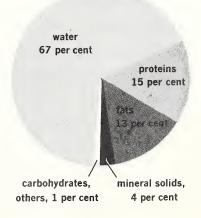
$$\begin{aligned} \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 + \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 &\to \mathbf{C}_{12}\mathbf{H}_{22}\mathbf{O}_{11} + \mathbf{H}_2\mathbf{O} \\ \text{glucose} & \text{fructose} & \text{sucrose} \end{aligned}$$

Or again, glucose can unite with galactose, and the result is lactose, milk sugar:

$$\begin{aligned} \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 + \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 &\to \mathbf{C}_{12}\mathbf{H}_{22}\mathbf{O}_{11} + \mathbf{H}_2\mathbf{O} \\ \mathbf{glucose} & \mathbf{galactose} & \mathbf{lactose} \end{aligned}$$

Because lactose, sucrose, maltose, and other 12-carbon sugars are each composed of two six-carbon sugars, they are called "double sugars," or disaccharides. Glucose and other six-carbon sugars in turn are called monosaccharides.

 ${f FIG.~6.1.}$ The average overall composition of protoplasm by weight.



Two or more disaccharides may combine into even longer chains, producing "multiple sugars," the polysaccharides already referred to in Chap. 2. Among polysaccharides important in protoplasm are *cellulose*, which is a chain of about 2,000 united glucose units; *starch*, a chain of 24 to 26-glucose units; and *glycogen*, a chain of 12- to 18-glucose units. Supermolecules of this sort are widespread derivatives of six-carbon carbohydrates.

Sugars may not only build up into larger molecules but may also break down into smaller ones. Under certain conditions, monosaccharides like glucose, for example, may decompose into fragments. Such carbohydrate breakdown is accompanied by release of energy, a phenomenon treated later in greater detail. At this point we merely note that one of the main functions of carbohydrates in protoplasm is to serve as *energy sources*.

Fats. Like carbohydrates, these are also composed of C, H, and O. We recall from Chap. 2 that a fat is a combination of glycerin and fatty acids. Glycerin, we have noted, is $C_3H_8O_3$; that is, the molecule is built around a three-carbon chain. Fatty acid molecules too are built around carbon chains, but here a chain may have varying length (Fig. 2.1). To form a fat molecule, three fatty acid molecules must be joined to one glycerin molecule:

3 fatty acid + 1 glycerin → 1 fat + 3H₂O

Note that three water molecules form as a byproduct here.

The properties of a fat are determined largely by the nature of the fatty acids it contains. If the acids are long carbon chains, the fat is likely to be a hard *tallow*. If they are short chains, the fat tends to be a volatile liquid or a semiliquid *oil*.

Chemically related to fats are the waxes, in which long fatty acids are joined to certain compounds other than glycerin. Also related to fats are sterols, complex ring structures which, as we shall see, form the framework of a number of vitamins and hormones. The general term lipid is often used to

designate the whole category of fatty, fatlike, and related substances.

The role of fats in protoplasm is manifold. Like carbohydrates, fats are energy-rich molecules. Energy is released by fat decomposition. Fats can also be transformed into carbohydrates, and vice versa. Fats, like carbohydrates and proteins, may be utilized as starting materials in the synthesis of more complex protoplasmic components. Finally, fats as such are fundamental structural building blocks of protoplasm. For example, they contribute to the framework of bounding membranes, where they probably play an important role in controlling movements of materials into and out of protoplasm.

Proteins. Besides C, H, and O, proteins always contain *nitrogen*, and usually sulfur as well. As noted in Chap. 2, proteins are made up of **amino** acids, which may be symbolized generally as

NH₂-R-COOH

Here —COOH is the group of atoms which gives an amino acid its acid properties, —NH₂ is the amino group, and —R— represents a ring or a chain of carbons holding H, OH, and other atoms. Amino acids consequently differ according to the nature of their —R— portions. In protoplasm, only 23 different kinds of such —R— portions are found. Hence there are just 23 different natural types of amino acids.

Proteins are long chains of joined amino acids. Consider how varied such chains can be:

- 1. They may contain any or all of the 23 different types of amino acids.
- 2. They may contain almost any number of each of these types.
- 3. The specific sequences in which given amino acids are joined can vary almost without restrictions.
- 4. The resulting chains can be folded two- and three-dimensionally in virtually any imaginable pattern.

The situation is rather like forming words and sentences from an alphabet of letters. In the English

language, 26 different letter symbols can be ordered practically at will to form an infinite variety of combinations. In proteins, the "letter symbols" are 23 different types of amino acids. And unlike real sentences, the protein "sentences" need not remain strung out in straight lines but can be branched and folded in practically any direction and form. Clearly, the number of theoretically possible proteins is astronomical.

Indeed, no two types of protoplasm contain the same types of proteins. This is not the case for carbohydrates or fats. A given complex carbohydrate, for example, is the same whether we obtain it from mushrooms or mangoes, from mice or from men. A given fat, similarly, is the same fat regardless of where we find it. Not so for proteins, however. Even twins have slightly different proteins, and the structural differences between proteins are the greater, the more unrelated two organisms are evolutionally. We say that proteins have a high degree of specificity: the proteins of a given protoplasmic unit have a unit-"specific" character; i.e., they are unique for that unit.

Some consequences of protein specificity are well known. For example, transfer of protein from one organism into the protoplasm of another amounts to the introduction of foreign bodies, and disease may result. Thus the proteins of plant pollen may produce allergy in human protoplasm; blood of one person mixed with blood of another, if not of compatible type, may produce protein shock and death; viruses and bacteria, partly because their proteins differ from ours, may produce many familiar disease reactions. A number of other significant consequences of protein specificity will be encountered later.

As a result of their complicated geometrical make-up, proteins are extremely sensitive to chemical and physical influences. Excessive heat, pressure, electricity, heavy metals, and many other agents produce protein coagulation. Here crosslinkages within the folded amino acid chain are broken, the exquisite geometry of arrangement is destroyed, and the molecule collapses (Fig. 6.2).

Mild disarrangement of a protein molecule is spoken of as denaturation. In living protoplasm, a denatured state may sometimes revert to the native state, and vice versa. But once coagulated, like boiled egg white, a protein usually cannot be restored to its native form. Protoplasmic death is sometimes a result of irreversible protein coagulation.

Among many functions of proteins, three have fundamental significance. Proteins are among the main structural building materials of protoplasm; proteins function as reaction-accelerating enzymes (see also below); and proteins help in the formation of other organic constituents, nucleoproteins in particular.

Nucleoproteins. We have found in Chap. 2 that these most critical constituents of protoplasm consist of nucleic acids and proteins; that nucleic acids are made up of many nucleotides; and that nucleotides in turn are either pyrimidine-sugar-phosphate or purine-sugar-phosphate:

pyrimidine or purine $\left.\right\}$ -sugar-phosphate = nucleotide many nucleotides \rightarrow nucleic acid nucleic acid + protein \rightarrow nucleoprotein

The sugar of a nucleotide is always one of two particular kinds. One kind is called ribose, the other desoxyribose. In both, five carbon atoms (not the usual six) form a chain; both sugars also are rather similar otherwise, but desoxyribose has one oxygen atom less than ribose. Now, in a given nucleic acid molecule, made up of hundreds of joined nucleotides, the sugars present are always of one kind. Thus one nucleic acid molecule may contain only ribose; another, only desoxyribose. On this basis we distinguish two categories of nucleic acids. One is called ribose nucleic acid or RNA for short; the other, desoxyribose nucleic acid, or DNA for short. As we shall see, RNA is found throughout a cell. But DNA occurs only in those nucleoproteins which form genes. Both RNA and DNA carry out

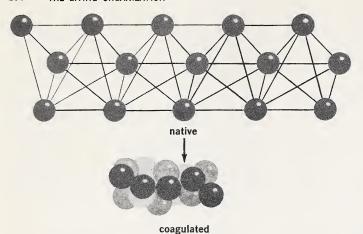


FIG. 6.2. The nature of protein coagulation. The upper figure represents a native protein, with a particular patterning and spacing of the amino acids. Coagulation involves the physical disruption of this patterning, as indicated in the lower figure. Note that coagulation does not change the chemical composition of the protein, only the physical.

vital specific functions, but we may note that it is the DNA type of nucleic acid which probably played the key role during the origin of life on this planet.

Different numbers and different sequences of nucleotides go into the make-up of RNA or DNA molecules (see Chap. 16 for detailed discussion). Therefore, as in proteins, the number of theoretically possible RNA's or DNA's is practically unlimited. We find, indeed, that RNA's and DNA's are *specific* like proteins; i.e., a given organism contains unique nucleic acids, and every other organism contains more or less different nucleic acids.

DNA and RNA are each joined to proteins, forming nucleoproteins. Little is as yet known about the nature of this union. But it should be easy to understand why, inasmuch as proteins and nucleic acids are separately enormously complex and varied, nucleoproteins are the most complicated chemical substances on earth. As we have seen, nucleoproteins were critical chemicals in the origin of life, and as we shall see later in detail, they have functioned ever since as the principal controllers of all living processes.

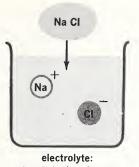
Carbohydrates, fats, proteins, nucleic acids and their various derivatives, together with water and other inorganic substances and numerous additional compounds found specifically in particular types of protoplasm, are the molecular bricks out of which living matter is made. By virtue of these bricks, protoplasm exhibits certain distinguishing chemical and physical properties. These properties demand our attention next.

THE PROPERTIES OF PROTOPLASM

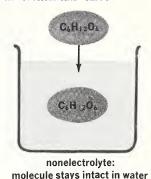
Considered separately, one by one, most properties of protoplasm are encountered also in inanimate systems and very few are uniquely protoplasmic. However, protoplasm is quite unique as a result of a particular *combination* of properties, and it is the combination which endows it with the potential of life. In the following, we shall be concerned with some of the individual properties which contribute to this living potential.

The most important of these properties is that protoplasmic molecules undergo large numbers of chemical reactions with one another. The presence of large amounts of water makes this especially possible. For water dissolves most of the other protoplasmic constituents, and chemical reactions take place particularly well in aqueous solution.

FIG. 6.3. Electrolytes and nonelectrolytes. Electrolytes (e.g., NaCl) break up in water into ions (Na+, Cl-), whereas nonelectrolytes (e.g., C6H12O6, sugar) remain intact molecules.



molecule ionizes in water



The solution now contains an equal number of

Protoplasm is not a static, passive material. Hundreds of reactions occur simultaneously every second, and through them, protoplasm is in continuous chemical turmoil. To the human observer, a tree may appear to be a rather placid, inactive structure. But if the tree's molecules could be seen, they would all be noted to be in constant, violent motion, colliding with one another and, as a result, reacting and changing. Consequently the tree as a whole changes continuously, and so indeed does every kind of protoplasm.

Another important property of protoplasm is that its molecules may occur in two different forms. As the following will show, they may be ionized or nonionized.

Ionization

When they are dissolved in water, as in protoplasm, some kinds of molecules do, and some do not, remain intact. Those which do not remain intact break up into two or more electrically charged atoms or groups of atoms, called ions. For example, table salt, sodium chloride (NaCl), is a mineral which ionizes. In protoplasm, or in water generally, it breaks up into a positively charged sodium ion (Na+) and a negatively charged chloride ion (Cl-):

such positive and negative ions, and it therefore remains electrically neutral as a whole. Electric neutrality is always preserved in solutions of ionized substances. But the presence of ions, rather than of whole molecules, makes possible the conduction of electric currents through the solution. Because of this, substances which ionize are also called electrolytes, and those which do not ionize, nonelectrolytes. Protoplasm contains both kinds. Most mineral substances are electrolytes, and they form ions. Sugars are good examples of nonelectrolytes (Fig. 6.3).

Depending on their chemical nature, different types of ions may carry different amounts of electric charge. One, two, or three charges, positive or negative, per ion are common. For example,

In the second equation above, note that sulfuric acid breaks up in such a way that *hydrogen ions* (H⁺) are produced. Any compound which breaks up so as to yield hydrogen ions is called an acid.

Analogously, any compound which breaks up so as to yield *hydroxyl ions* (OH-), as in the third equation above, is a base, or an alkali.

A compound resulting from the chemical interaction of an acid and a base is a salt. Sodium chloride (NaCl) is a salt because it is formed by the interaction of hydrochloric acid (HCl) and sodium hydroxide (NaOH):

$$HCl + NaOH \rightarrow NaCl + H_2O$$

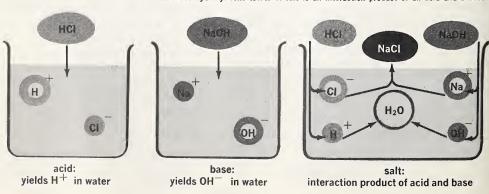
acid base salt

If a substance is an electrolyte, it is either an acid or a base or a salt (Fig. 6.4). Chemists distinguish between "strong" acids and "weak" acids, strong bases and weak bases, and strong salts and weak salts. The basis for such distinctions is the *extent* to which an electrolyte is ionized. In a strong acid, for example, all, or practically all, the acid molecules are ionized. In a weak acid, on the other hand, only a few of the acid molecules are ionized; the others remain intact as molecules. The situation is analogous for bases and salts.

It is often important to determine the "strength" of a solution of electrolytes, i.e., its degree of acidity or alkalinity. This can be done with appropriate electrical apparatus, by measuring the relative number of H+ and OH- ions present in the solution. The result is expressed as a number, called the pH of the solution. Numbers indicating pH range from 0 to 14. A pH of 7 indicates chemical neutrality; that is, the solution is neither acid nor basic because the number of H+ ions equals the number of OHions. The lower than 7 the pH of a solution, the more acid it is; that is, there are more H+ ions present than OH- ions. Conversely, the higher than 7 the pH, the more alkaline is a solution. Thus the maximum possible acidity is indicated by pH 0, and the maximum possible alkalinity, by pH 14 (Fig. 6.5).

Protoplasm, containing a mixture of ionized acids, bases, and salts, has a pH usually very near neutrality. For example, the pH of human blood is 7.3. However, some types of protoplasm may be characteristically more acid (e.g., lemons) or basic (e.g., many pond organisms). A living system does not tolerate significant variations of its normal acid-base balance, and its pH must remain within fairly narrow limits. If these limits should be exceeded, major chemical and physical disturbances would

FIG. 6.4. When placed into water, an acid releases hydrogen ions (H^+) and a base releases hydroxyl ions (OH^-). A salt is an interaction product of an acid and a base.



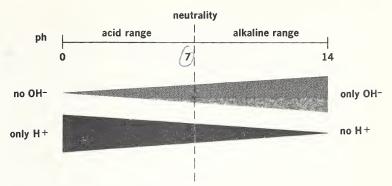


FIG. 6.5. The pH scale.

result which could be lethal. For example, protoplasmic proteins would be coagulated.

Proteins are themselves responsible for another important general property of protoplasm: some proteins function as reaction-accelerating *enzymes*.

Enzymes

As noted in earlier contexts, a chemical reaction can occur only if molecules (or ions) come into direct contact with one another by collision. It follows that the more frequently given molecules collide, the faster can be the reaction among them. Molecular collisions ordinarily are produced by heat. The heat energy of the environment causes molecules to vibrate uninterruptedly, in random motions. The higher the temperature, the more violent are the molecular motions. Ordinary room temperature sometimes provides sufficient heat to agitate given molecules enough to allow them to react. But for many reactions room heat is quite insufficient. For example, a mixture of fat and water reacts so slowly at room temperature that the result is quite unnoticeable. However, one can increase the molecular collisions, hence the speed of reaction, by subjecting the mixture to higher temperatures, e.g., over a flame.

In protoplasm, most vital chemical reactions could occur only if environments were far hotter than room temperature. The fat-water reaction, for example, occurs in protoplasm very often, but from the above we should expect the body temperature to be far higher than it actually is. It is true generally that most living reactions could occur sufficiently fast only if protoplasm were at boiling temperatures, but that of course would kill living matter. How then are enough molecular collisions brought about in protoplasm despite the low temperatures at which it must exist? The answer lies in speeding up reactions without heat, by means of so-called catalysts.

Catalysts are chemicals of very diverse kinds, and they are used frequently by chemists who wish to speed up a particular reaction without heating it. Catalysts occur in protoplasm too. They are all proteins, and they are called enzymes.

Virtually every one of the thousands of protoplasmic reactions is speeded up enormously by a particular enzyme protein. Without such enzymes, the reactions could not occur fast enough at ordinary temperatures to sustain life. Thus enzymes are a device through which reactions requiring high temperatures in test tubes can occur at low temperatures in protoplasm.

How does an enzyme work? Best available evidence indicates that it combines temporarily with the reacting molecules. Mutual contact of these molecules is then no longer a matter of chance collision but a matter of certainty. Hence faster reaction.

The protein nature of enzymes is essential to this reaction-accelerating effect. As already pointed out, protein molecules are huge, and they each consist of very many joined, variously arranged amino acids. Hence, according to its particular internal structure, a protein has one of an almost infinite number of overall physical shapes. It also has a unique surface shape, distinct from that of other types of proteins. The nature of the surface appears to be the key to enzyme action. Consider the reaction

glucose + fructose → sucrose

Glucose has a given unique surface shape, and so does fructose. Enzymatic acceleration of this reaction may now occur if the surfaces of both glucose and fructose happen to fit closely into the surface of a particular protein molecule. In other words, if the reacting molecules can become attached to a suitably shaped surface of an enzyme, then these molecules will be so close to each other that they may react chemically (Fig. 6.6). The enzyme itself remains relatively passive here. It only provides a uniquely structured "platform" on which particular molecules may become trapped. Such trapping brings reacting molecules into contact far faster than chance collision at that temperature. Hence accelerated reactions. Held by the enzyme, glucose

FIG. 6.6. The surfaces of molecules A and B fit into the surface of the enzyme. Reaction between A and B is thus speeded up, for contact between A and B now does not depend on chance collision.



and fructose react and become sucrose, and sucrose then disengages from the enzyme surface. We may think of this as a "lock-and-key" process. Only particularly shaped keys fit into particularly shaped locks. Just so, only certain types of molecules will establish a close fit with a given type of enzyme

This undoubtedly explains the phenomenon of enzyme specificity; that is, a given type of enzyme normally can accelerate only one particular type of reaction. For example, the enzyme in the glucosefructose reaction above (called invertase) is specific and catalyzes only that particular reaction. In protoplasm, there are actually almost as many different kinds of enzymes as there are different kinds of reactions. This specificity of enzymes is a consequence of the more general phenomenon of protein specificity, which we have already discussed earlier. Because of protein specificity, some proteins are enzymes and some are not. For if a protein happens to have a surface into which some other molecules could fit, then that protein could function as an enzyme in reactions involving those molecules.

Several other characteristics of enzymatic reactions may now be noted. Inasmuch as an enzyme essentially functions as a passive reaction platform, it is not itself changed by the reaction. It reappears unchanged at the end of the reaction, free to combine with a new set of starting molecules. Because of this, very small amounts of enzymes, used over and over, can catalyze large quantities of given raw materials.

Note also that a given enzyme can speed up a reaction in either direction. The reaction sucrose -> glucose + fructose is accelerated by the same enzyme, namely, invertase, that speeds up the reaction glucose + fructose → sucrose. This is understandable again if we keep in mind that enzymes are primarily passive reaction platforms. Thus enzymes only influence reaction speeds; other factors govern the direction of a reaction.

Enzymes share the chemical and physical properties of proteins generally. Like all proteins, individual enzyme molecules wear out or break down, even under normal conditions. They must be replaced by resynthesis from raw materials—reactions which themselves require enzymes. Like all proteins also, enzymes are extremely sensitive to changes of temperature, pH, pressure, metallic poisons, and other agents. Coagulated enzyme proteins usually are not effective catalytically, undoubtedly because coagulation destroys the unique surface shape of the molecule.

Enzymes may be classified according to the kind of molecule they affect. For example, any enzyme accelerating reactions of carbohydrates is called a carbohydrase. Invertase, above, is a carbohydrase. Analogously, proteinase and lipase, for enzymes catalyzing reactions of proteins and of fatty substances (=lipids), respectively. A suffix -ase always signifies that the substance in question is an enzyme. Note, however, that names of enzymes need not necessarily end in -ase.

In writing an enzymatic reaction symbolically, the name of the enzyme is conventionally put over the reaction arrow. Thus

invertase
glucose + fructose → sucrose

As we have seen, the presence of ions and enzymes endows protoplasm with certain *chemical* properties. Its particular chemical composition also endows protoplasm with certain *physical* properties, and some of these we shall now examine.

The colloidal state

Clearly, protoplasm is neither a true solid nor a true liquid but a system composed of both solid and liquid components. Any such system can be classified as belonging to one of three categories, depending on the size of the solid particles. If all particles are very small, for example, small ions or molecules, then the system is a true solution. Crystals can readily form from it, and such a system is therefore also called a *crystalloid*. If all particles are very large, e.g., the size of soil grains, they soon settle out by gravity at the bottom of a container.

Such a system is a coarse suspension. But if all particles are of intermediate size, they neither form a solution, i.e., do not easily crystallize, nor do they settle out. Such a system is a colloid.

Protoplasm is largely a colloidal system. It consists of a *liquid phase*, namely, water containing dissolved ions and small molecules, and a *dispersed phase*, namely, very large molecules, including proteins and others, and aggregates of molecules.

What are some of the properties of colloids? What, first, prevents colloidal particles in protoplasm from settling out?

As noted above, the molecules of a liquid vibrate continuously, the more so the higher the temperature. When the liquid freezes, this molecular motion is reduced sharply. Above the boiling point, molecules move so rapidly that many escape; i.e., the liquid vaporizes at great rate. If dispersed particles are present in a liquid, they are buffeted and bombarded constantly by the molecules of the liquid. Very large particles are unaffected by these tiny forces, and they fall straight to the bottom of a container. But smaller colloidal particles may be pushed back and forth, up and down. Gravitational pull may thereby be counteracted partly or wholly, and the particles thus may be kept suspended. This random movement of small particles is called Brownian motion. It is easily demonstrable under the microscope.

Brownian movement aids in keeping colloidal particles from settling out, but they cannot remain suspended by this force alone. Colloids stay dispersed mainly because of their electric charges. All solid particles of a given colloidal system are either electropositive or electronegative. Since like charges repel, the particles are kept apart. If the charge is neutralized by electricity of opposite type, the colloid particles do settle out (Fig. 6.7).

Protoplasmic colloids undergo reversible sol-gel transformations, also called *phase reversals*. If large numbers of particles are added to a colloid, or alternatively, if water is gradually withdrawn, the particles are brought closer together and they come into contact with one another eventually. Rod-

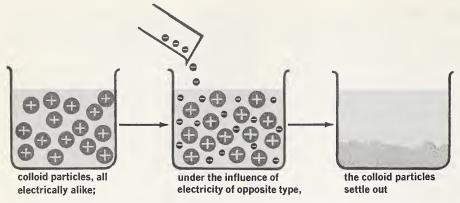


FIG. 6.7. Colloid particles carry similar electric charges—in this illustration, positive ones (left). These charges make the particles repel one another, and so keep them suspended. If electricity of opposite type is added (middle), the colloid charges are neutralized and the particles settle out (right).

shaped particles then pile up like a log jam; round or irregular particles interlock in intricate ways. In effect, the original dispersed phase now is a continuous spongelike network which holds water within its meshes, in discontinuous droplets. This is the gel state of a colloid. The quasi-solid, pliable aspect of protoplasm, as in skin or muscle, or of protein colloids generally, as in Jello and gelatin, is due to the gel condition. We may understand, therefore, how even organisms like jellyfish, which contain as much as 90 per cent or more water, can maintain definite form and shape.

Conversely, addition of water to a colloidal system, or removal of dispersed particles, results in greater fluidity, the sol state of a colloid (Fig. 6.8). In protoplasm, sol and gel states alternate normally and repeatedly in accordance with local variations of particle concentrations. Boundary protoplasm is more or less permanently in a gel state.

Increased temperature may convert a gel into a sol. For at higher temperature, colloidal particles in a gel become more agitated and the gelled meshwork is disrupted (e.g., liquefaction of Jello by heating). Many other physical and chemical influences, such as low or high pH or pressure, affect sol-gel conditions. For example, cream, a sol, when churned (i.e., when put under pressure), yields butter, a gel. Butter in turn can be creamed, that is, returned to the sol state.

Migratory movements occur in colloids, and also in true solutions, as a direct result of the heat motion of the particles. If ions, molecules, or colloidal particles are unevenly distributed, more collisions will take place in the more concentrated regions. For example, if a particle in the circle in Fig. 6.9 is displaced by heat motion, or by Brownian bombardment, toward a region of higher concentration, it will soon be stopped in its track by collision with other particles. But if it is displaced away from a high concentration, its movement will not be interrupted as soon, since neighboring particles are farther apart. On an average, therefore, a greater number of particles is displaced into more dilute regions than into more concentrated ones. In time, particles throughout the system will become distributed evenly. This equalization resulting from migration of particles is called diffusion.

Diffusion plays an important role within proto-

plasm. For example, it happens often inside a cell that particles are unevenly distributed. Diffusion will then tend to equalize the distribution. Evidently, this is one way through which materials in protoplasm can migrate about.

An important property of protoplasm resulting from its colloidal make-up is that, as the following will show, it tends to form *membranes*.

Protoplasmic membranes

The boundary between a colloidal system and a different medium (air, water, solid surfaces, or another colloid of different type) is called an *interface*. The molecules there are usually subjected to complex physical forces, with the result that the molecules at the interface pack together tightly and become *oriented* in layers. A so-called *interfacial membrane* forms (e.g., the "skins" on puddings, custards, boiled milk). On surface protoplasm, as on the surfaces of cells, for example, such molecular skins are called **plasma membranes**. If the plasma membrane on the surface of a cell is punctured, a new membrane develops over the opening within seconds, before appreciable amounts of the interior can flow out.

Protoplasmic membranes are the gateways through which the molecular traffic into and out of protoplasm must pass. How do materials get through such membranes?

Plasma membranes have different permeability to different substances. Most membranes are completely permeable to water; that is, water molecules can pass through freely in either direction. As for other materials, organic or inorganic, there is no rule by which their passage potential can be determined beforehand. In general, three classes of materials can be distinguished: those that can pass through a membrane in either direction; those that can pass in one direction but not in the other; and those that cannot penetrate at all. These categories vary considerably for different membranes.

In the past, traffic through living membranes has been compared with traffic through nonliving ones, like cellophane. Such nonliving membranes let

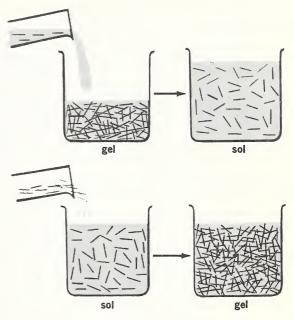
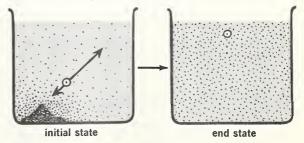


FIG. 6.8. Phase reversals. A gel may be transformed into a sol either by adding more liquid (top) or by withdrawing solid particles. And a sol may be transformed into a gel either by adding more solid particles (bottom) or by withdrawing liquid.

FIG. 6.9. Diffusion. In the initial state, particles are distributed unevenly. A given particle (for example, the circled one) will therefore have more freedom of movement in the direction of lower concentrations. This eventually leads to an even distribution of particles, as in the end state shown at right.



water or small ions through, but not proteins, for example. Particle penetration here can be explained rather readily in terms of diffusion. Ions, for example, would strike the barrier; most of them would bounce off, but some would pass through pores in the membrane. If the ion concentration is greater on one side of the membrane than on the other, more ions on an average would migrate into the dilute side, thus equalizing concentrations.

However, a hypothesis postulating diffusion through pores is generally inadequate for living membranes. If protoplasmic membranes were indeed passive, inert films with holes, like cellophane, then it should not matter if such a membrane were poisoned. For being nonliving, it could not be affected by a poison. But experiments actually show that the activity of protoplasmic membranes is stopped or severely impaired by poisons, indicating that such membranes are not simply passive films. Moreover, if living membranes actually contained small holes, then the size of a particle should determine whether or not it could go through such holes. However, particle size often is of little importance in protoplasmic membranes. For example, under certain conditions large protein molecules may pass through a given membrane whereas very small molecules sometimes may not. Again, the molecules of the three sugars glucose, fructose, and galactose, all C₆H₁₂O₆, have the same size, yet they are passed through living membranes at substantially different speeds.

Clearly, membranes are highly selective, that is, they act as if they "knew" which substances to transmit and which to reject. Moreover, it is now known that active, energy-consuming work is often done by a living membrane in transmitting materials and that complex chemical reactions take place in the process. Therefore, rather than visualizing a passive membrane with small holes, we are led to regard plasma films as dynamic living structures in which entering or leaving particles are actively "handed" across from one side to the other.

Hence, if we encounter a situation where materials other than water pass through a protoplasmic membrane, we would be quite wrong in simply

saying offhandedly that this can be explained by "diffusion." Diffusion does play *some* role in most cases, but actually a minor one; active work by the membrane usually plays the all-important role.

Membranes also account for a final protoplasmic property we must discuss.

Osmosis

When a protoplasmic membrane separates one colloid from another, or from a different kind of medium, it may happen that on either side of the membrane are present, in addition to water, particles which *cannot* go through. Suppose that one side contains a very low concentration of such particles (side A in Fig. 6.10), and the other side a very high concentration (side B, Fig. 6.10). What events occur in such a system?

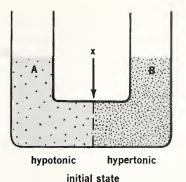
- 1. In the beginning, relatively more water molecules are in contact with the membrane X on the A side than on the B side, since fewer of the solid particles occupy membrane space on the A surface than on the B surface.
- 2. Therefore, more water molecules, on an average, diffuse through the membrane from A to B than from B to A.
- 3. As a result, the water content decreases in A and increases in B. Particles in A become crowded into a smaller and smaller volume, and more and more of them therefore take up membrane space on the A surface. On the B side, the increasing water content permits the spreading of the particles into progressively larger volumes, thus reducing particle concentration along the B surface of the membrane.
- 4. A stage will be reached at which the number of particles along the A surface equals that along the B surface. From then on, the number of water molecules diffusing from A to B equals the number diffusing from B to A. Thereafter, no further net shift of water occurs.

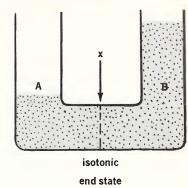
This movement of water is called osmosis.

Note that the degree of osmosis depends on the concentration differential, the relative numbers of particles, in A and B.

If the difference in particle number is great enough (for example, if A contains pure water only

FIG. 6.10. Osmosis. In the initial state, because A is less concentrated than B, water will be pulled from A into B. This eventually leads to the isotonic end state, where concentrations in A and B are equal. From this point on, no further net migration of water occurs; that is, just as much water moves from A into B as from B into A. A semi-permeable membrane is represented by X.





and B contains water and a large number of particles), then the A side may dehydrate completely and collapse while the B side might burst and so collapse also. The side which loses water in osmosis is generally said to be hypotonic, and the side which gains water, hypertonic. When neither side gains nor loses water, i.e., when both sides contain equal concentrations of particles and thus are in osmotic equilibrium, they are said to be isotonic to each other.

Note that the net effect of osmosis is to pull water into the region of higher concentration, i.e., from the hypotonic to the hypertonic side. The process will continue until the two sides are isotonic. And note that osmosis will occur whenever certain particles cannot or do not pass through a membrane. Then nothing migrates through the membrane except water (plus any particles present which can diffuse through).

Like diffusion, osmosis plays an important role in protoplasm. It is one agency by which water is distributed and redistributed across membranes. But note that, as in diffusion, care must be taken in explaining given membrane phenomena simply as "osmosis." Sometimes the event in question actually is osmosis, but many times it is not. In this connection, it is particularly poor practice simply to dismiss given events at membranes unthinkingly as 'diffusion and osmosis."

Many well-known phenomena do have an osmotic

basis. For example, the laxative action of epsom salt (magnesium sulfate, MgSO₄) results from the impassability of this molecule through the gut wall. Consequently, water is pulled osmotically from the body tissues into the gut cavity, softening the feces. In another instance, the drinking of sea water greatly increases the salt concentration of the blood. Water is then pulled from the body tissues into the blood, body protoplasm dehydrates, and thirst is therefore greater than ever. Water containing 0.9 per cent NaCl, or an equivalent total of other particles, is isotonic to human protoplasm. Such a medium is called a *physiological saline* solution and must be used when drugs, glucose, or other substances are injected by physicians.

We may now summarize all the foregoing, and we may describe some of the properties of protoplasm as follows. Chemically, the water component dissolves most of the other components and maintains many of them in an ionized state. Protoplasm so becomes a complex mixture of acids, bases, salts, and nonelectrolytes. Some of the protein components in this mixture function as enzymes. These, plus the temperature of the environment, permit numerous reactions at various speeds, in various directions, and in various amounts. As a result of such reactions, energy exchanges occur, concentrations change, and chemical composition as such becomes changed.

New sets of reactions now become possible among

the altered constituents, and such reactions alter chemical conditions in turn. If, as is normally the case, changes in the external environment occur at the same time, the diverse chemical events in protoplasm will be affected accordingly. Living matter consequently is forever in chemical flux. Perhaps the most remarkable outcome of these uninterrupted processes is that protoplasm remains "living" throughout.

Accompanying and greatly influencing these many chemical events are physical ones. In physical terms, protoplasm may be described as a mixed colloidal system, bounded by variously permeable membranes, undergoing localized sol-gel transformations, and being kept in constant internal motion by the heat of the environment, by molecular bombardments, by diffusion displacements, and by osmotic forces. As a result of these properties, living matter is subjected to a continuous physical flux equally as profound as the chemical flux. Indeed, physical changes initiate chemical ones, and vice versa. From any small-scale point of view, therefore, protoplasm is never the same from moment to moment.

Furthermore, the small-scale properties of protoplasm, chemical and physical, materially influence every larger-scale property. As an important case in point, protoplasm does not occur in bulky, continuous masses. Rather, the tendency of the living colloid to form membranes leads to a subdivision of protoplasm into small, discontinuous globules. These have a certain individuality, and they are kept physically separated from one another by their surface membranes. Globules of this sort represent cells. We shall examine these universal structural units of protoplasm in the following section.

THE STRUCTURE OF PROTOPLASM

As a result of the uninterrupted chemical and physical flux within protoplasm, the contents of a living cell are always in actual, often observable motion. New materials enter a cell continuously, wastes and manufactured products leave continuously, and substances in the cell interior are con-

tinuously transformed chemically and redistributed physically. Therefore, as cells function, such functioning invariably means change of structure. And we may note that the idea of structure, quite like that of function, has an important progressive, historical aspect which cannot be dissociated from the dimension of time. But although cells change with time, certain general features must remain invariant if cells are to be living at all. These common invariant features of all cells will occupy our attention.

Fundamental structure

The generalization that all living organisms consist of cells and cell products is known as the cell theory. Principal credit for its formulation is usually given to the German biologists Schleiden and Schwann, whose work was published in 1838. But the French biologist Dutrochet had made substantially the same generalization as early as 1824. The cell theory rapidly became one of the fundamental cornerstones of modern biological science, and, with minor qualifications, it still has this status today.

Cells came to be recognized early as the "atomic" units of living matter, structurally as well as functionally. In 1831, Robert Brown discovered the presence of nuclei within cells, and in 1839 the Bohemian biologist Purkinje coined the general term "protoplasm" for the living substance out of which cells are made. Virchow in 1855 concluded that "omnis cellula e cellula"-new living cells can arise only by reproduction of preexisting living cells. This important recognition of the continuity of life, and thus of the direct derivation of all cells from ancient cellular ancestors, introduced the notion of history into the study of cells. Ever since, cell biology has revolved around three interrelated problems: cell structure, cell function, and shortand long-range cell development. The first of these concerns us here particularly.

Examination of living or killed cells by various kinds of microscopes shows that cells vary considerably in size, ranging in diameter from about 2 microns to as much as several millimeters and more (1 micron, $1 \mu = 1/1,000 \text{ mm}$). However, the order of size of the vast majority of cells is remarkably

uniform. A diameter of 5 to 15 μ is fairly characteristic of cells generally. We surmise that, notwithstanding the exception, cells can be neither much smaller nor much larger than a certain norm. Too small a size presumably would not provide enough room to accommodate the necessary parts, and too large a size would increase the maintenance problem and at the same time reduce the efficiency of compact operation.

The two fundamental subdivisions of virtually all cells are the nucleus and the protoplasm surrounding the nucleus, called the cytoplasm. The nucleus is bounded by a nuclear membrane, the cytoplasm by a cell membrane, also called plasma membrane (Fig. 6.11). Most cells contain a single nucleus each. But there are many exceptions. As already noted in Chap. 2, the Monera do not contain nuclei at all. Conversely, many other single-celled organisms normally contain more than one nucleus. Binucleate and multinucleate cells are found also with some frequency among multicellular organisms.

There are exceptions too concerning the individuality of cells, normally maintained by the cell membrane. In certain tissues among many young

or embryonic organisms, cell membranes at first form boundaries between individual cells. But at a later stage of development, these membranes dissolve and the tissue becomes a fused, continuous protoplasmic mass, with nuclei dispersed through it. Such a structure, in which cellular individuality has been lost, is called a syncytium.

Despite variations in the number of nuclei, or the occasional loss of the structural discreteness of cells, the fundamentally cellular character of living matter is undeniable even in such exceptional cases. And in all other cases the cellular character is unequivocal, for there we deal with distinct bits of protoplasm, each bounded by a plasma membrane and containing one nucleus.

Nucleus and cytoplasm

A nucleus typically consists of three kinds of components: the more or less gel-like nuclear sap, or nucleoplasm, in which are suspended the chromosomes, and one or more nucleoli (Fig. 6.12). The chromosomes are the principal nuclear structures. Indeed, a nucleus as a whole may be regarded primarily as a protective housing for these slender, threadlike bodies. Chemically, chromosomes consist

FIG. 6.11. The general structure of cells. The diagram represents a section through a cell, and the photo shows red blood cells of a bird. Note the darkly stained central nucleus of each blood cell. (Photo, General Biological Supply House, Inc.)

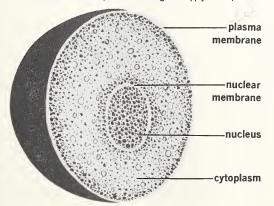






FIG. 6.12. Electron micrograph of a cell nucleus. The whole elliptical structure is the nucleus; cytoplasm is outside it. Note the nuclear bounding membrane. Within the nucleus, the large dark patch is the nucleus and the dark speckles are the genecontaining bodies ("chromatin"). (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)

largely of protein and of nucleoprotein; DNA is the principal nucleic acid of the nucleoproteins, but some RNA is usually also found. Functionally, chromosomes are the carriers of the genes, which, as noted on several previous occasions, are the ultimate controllers of all cellular processes. Monera do not contain formed nuclei, as we have seen, and thus they probably do not contain chromosomes like other cells, but all cell types contain genes.

Chromosomes are conspicuous only during cell reproduction, when they become thickly coated with additional nucleoprotein. At other times such coats are absent, and chromosomes then are very fine filaments not easily identifiable within the nuclear sap. The exact number of chromosomes within each cell nucleus is an important species-specific trait. For example, cells of human beings

contain 46 chromosomes each (in earlier years the number was thought to be 48, but recent research has established the actual number as 46). Analogously, cells of every other type of organism have their own characteristic chromosome number. A cell rarely contains more than in the order of 100 chromosomes. Hence, since there are several million different species of organisms, many species share the same chromosome number. But note that possession of the same numbers of chromosomes does not mean possession of the same kinds.

A nucleolus ("little nucleus") is a spherical body which also consists largely of nucleoprotein. But the only type of nucleic acid present here is RNA. As we shall see in a later chapter, nucleoli are derivatives of chromosomes and they appear to play an important role in the control of protein synthesis



FIG. 6.13. Electron-micrographic close-up of a nuclear membrane. Note the double-layered condition of the membrane. The arrow points to one of the pores which characterize such membranes. (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)

within cells. Given cell types contain a fixed number of nucleoli per nucleus.

The whole nucleus is separated from the surrounding cytoplasm by the nuclear membrane. This structure, like most other protoplasmic membranes, is constructed mainly of proteins and fatty substances. It governs the vital traffic of materials between cytoplasm and nucleus (Fig. 6.13).

If the nucleus, by virtue of its genes, is the control center of cellular functions, then the cytoplasm is the executive center. In it, the directives of the nucleus are carried out. But it should be emphasized at once that such a functional distinction between nucleus and cytoplasm should not be taken too rigorously. Although the nucleus primarily controls, it also executes many directives of the cytoplasm; and although the cytoplasm primarily executes, it also influences many nuclear processes. As we shall see later, a vital reciprocal interdependence binds nucleus and cytoplasm and experiment has repeatedly shown that one cannot long survive without the other.

Cytoplasm consists of a semifluid ground substance, which is in a sol or a gel state at different times and in different cellular regions and in which are suspended large numbers of various formed

inclusions. Such inclusions may be shaped into granules, rodlets, filaments, or droplets. Each of these may have various sizes and chemical compositions and may have a variety of functions. Particular cell types often possess unique inclusions not found elsewhere. The following inclusions are widespread among many or all cell types:

Mitochondria. Found universally in all cells, these round or filamentous structures are known to contain respiratory enzymes, that is, enzymes required in energy-producing reactions. Mitochondria are the principal chemical "factories" in which cellular respiration is carried out (Fig. 6.14; also Chap. 13).

Microsomes. As suggested by their name, these are exceedingly tiny granules, visible under the

FIG. 6.14. Electron micrograph of cytoplasm, showing mitochondria (sausage-shaped bodies) and microsomes (faint beaded chains). The small black granules are fatty material. The gray background in the photo represents the viscous ground substance in which all cytoplasmic bodies and particles are suspended. (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)



electron microscope (Fig. 6.14). Present in all cells, they contain RNA-nucleoprotein and enzymes required in many synthesis reactions. It is believed that microsomes are the principal factories in which cellular protein synthesis is carried out.

Golgi bodies. The electron microscope shows these structures to be made up of bundles of parallel, very fine membranes (Fig. 6.15). Golgi bodies are particularly conspicuous in cells which produce special secretions, such as gland cells. From this, it is believed that the Golgi structures play an important role in the manufacture of secretion products.

Plastids. These round or oval bodies are found in most photosynthesizing cells. A plastid may contain pigment, and if the pigment is *chlorophyll*, then the plastid is given the name *chloroplast*. In addition to chlorophyll, chloroplasts contain nucleoprotein, enzymes, and all other chemical machinery for photosynthesis.

Centrioles. In most Protista and in all animal cells (but not in advanced plants) a single centriole is located just outside the nucleus. We shall find later that this small granule functions in cell reproduction.

Apart from the inclusions just listed, cytoplasm generally contains additional granules and fluid-filled droplets bounded by membranes, called vacuoles. Such cytoplasmic granules and vacuoles perform a large variety of functions. They may be vehicles transporting raw materials from the cell surface to interior processing centers (e.g., food vacuoles) or finished products in the opposite direction (e.g., secretion granules); they may be places of storage (e.g., starch granules, fat vacuoles, water vacuoles); they may be vehicles transporting waste materials to points of elimination (e.g., excretory vacuoles); or they may be special processing centers themselves.

In addition to all these, cytoplasm may or may not contain a variety of long, thin fibrils, made

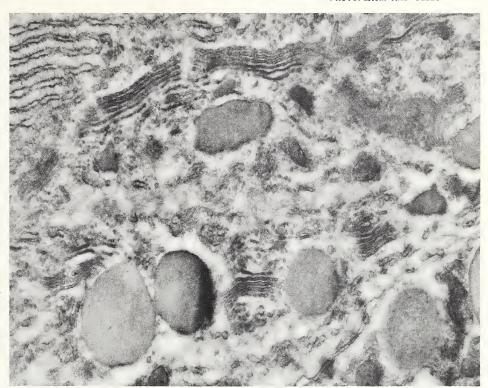


FIG. 6.15. Golgi bodies. In this electron micrograph of a portion of a mucus-secreting cell of the frog, the Golgi bodies appear as bundles of parallel lamellae. The large round bodies are secretory granules. (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)

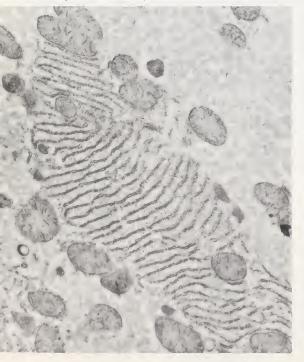
predominantly out of protein (e.g., contractile fibrils, neurofibrils). Various other inclusions, unique to given cell types and serving unique functions, may also be present. In general, every function a cell performs, common or not, is based on a particular structure in which the machinery for that function is housed.

Cytoplasm as a whole is normally in motion. Irregular eddying and streaming occur at some times, and at others the substance of a cell is subjected to cyclical currents, a movement known as

cyclosis. The formed inclusions, as well as the nucleus, are swept along passively in these streams. The specific cause of such motions is unknown, but there is little doubt that they are a reflection of the uninterrupted chemical and physical changes which take place on the molecular level. Whatever the specific causes may be, the apparently random movements might give the impression that nothing is fixed within a cell and that cytoplasm is simply a collection of loose particulate bodies suspended in "soup."

But this impression is erroneous, as examination under the electron microscope shows. The ground substance of cytoplasm, which under the light microscope does appear to be a fluid, structureless "soup," actually turns out to be highly structured and organized. A network of exceedingly fine membranes can be shown to traverse the cytoplasm from plasma membrane to nuclear membrane. This network is known as the endoplasmic reticulum (Fig. 6.16). Linked to it are the mitochondria, the microsomes, and all the other cytoplasmic inclusions. Thus little is really "loose" in a cell. When cytoplasm as a whole

FIG. 6.16. An electron micrograph of a portion of the endoplasmic reticulum of a rat liver cell. Note that the reticulum is made up of an array of double membranes. The oval bodies around the reticulum are sections through mitochondria. (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)



streams and moves, the endoplasmic reticulum streams and moves too, and the formed inclusions are carried along, still held to the ultramicroscopic network. Evidently, even though the contents of a cell may shift position and the cell as a whole may be deformable, an orderly structural integration of the interior persists nevertheless. Indeed, this is essential if cellular functions are to be orderly and integrated.

The cell surface

The cell as a whole is bounded by a cell membrane. Composed predominantly of protein and fatty substances, this important structure is far more than a passive outer skin. It is an active, highly selective, semipermeable membrane, which regulates the entry and exit of materials into and out of a cell. The membrane therefore plays a critical role in all cell functions, since, directly or indirectly, every cell function necessitates absorption of molecules from the exterior and/or excretion of molecules from the interior. We shall have occasion in many later contexts to consider some of the specific activities of cell membranes.

In given cell types, additional structures may be present on or around the cell membrane. Such surface structures serve variously in mechanical support, in protection, and in locomotion. For example, plant cells secrete cell walls around their plasma membranes. These walls, made of cellulose, are fairly rigid envelopes which maintain cell shape and aid in support against gravity. Plant cells exposed directly to the external air also secrete cuticles, in addition to cell walls. Such cuticles are made of wax and other waterproofing materials. Cellulose and wax are not found among animal cells, but in many cases they too surround themselves with walls or cuticles. For example, a coat of chitin, a complex organic material, is found on the skin cells of insects and many other invertebrates. Analogously, the surface cells of mammalian skin and hair secrete external coats made of the protein keratin. Skeletal shells, of lime, glass (silica), or organic substances, are among other external covers manufactured by many cell types.

The principal locomotor structures on the surfaces of cells are cilia and flagella (Fig. 6.17). Both are slender, filamentous projections, and both have similar internal structure. The electron microscope reveals each cilium or flagellum to be a complex bundle of exceedingly fine fibrils. Flagella are usually longer than cilia. A flagellate cell generally carries but one or a few flagella, but a ciliated cell may carry hundreds of cilia. Complex systems of special granules and fibrils, located just under the cell membrane, hold the filaments in place and control their motion. Cilia and flagella are found widely among Protista, where they are the major means of propulsion and of creating food-bearing currents in the external water environment. Cilia and flagella are also widespread among other plants and animals. For example, the sperm cells of all but the most advanced plants move by means of flagella. Many embryos, larvae, and small adult animals move by means of ciliated skins. And many animal tissue cells, like those lining the ducts of the breathing and reproductive systems, possess ciliated surfaces.

We have outlined some of the key structural features characteristic of cells generally. As we have seen, certain of the components of the nucleus, the cytoplasm, or the cell surface may be associated directly with well-circumscribed cell functions. Photosynthesis and respiration, for example, are distinct functions performed in distinct cytoplasmic structures. See Table 4 for a summary of such correlations. But many cell functions cannot be localized so neatly. For example, cellular reproduction requires the cooperative activity of many or all of the cell components present. Functions of this kind cannot be referred to any particular part of a cell, but only to the cell as a whole.

Note in this connection that whereas many cell structures are bulky enough to be visible under the microscope, even more are not visible: individual molecules in a cell "function" no less than larger molecular aggregates. Note also that *each* cellular structure performs a function, and as the structures differ among cells, so do the functions.



FIG. 6.17. The ciliate protozoon Tetrahymena, stained to show the cilia and their arrangement on the body surface. (Courtesy of Dr. Norman Williams, Iowa State University.)

 TABLE 4.
 Some structural components of cells and their correlated functions

Structure	Function	
Nucleus		
Chromosomes	Ultimate control of cell activities	
Nucleolus	Control of protein synthesis	
Nuclear membrane	Traffic control to and from cyto- plasm	
Cytoplasm	-	
Mitochondria	Site of respiration	
Microsomes	Site of protein synthesis	
Golgi bodies	Site of secretion synthesis (?)	
Chloroplasts	Site of photosynthesis	
Centrioles	Auxiliary to cell division	
Granules /	Transport, storage, processing	
Vacuoles \$	centers	
Fibrils	Contraction, conduction	
Surface		
Plasma membrane	Traffic control to and from cell	
Cell walls { Cuticles	Protection, support, cell shape	
Cilia Flagella	Locomotion, current creation	

REVIEW QUESTIONS

- 1. What inorganic constituents occur in protoplasm, and in what forms? What are organic compounds? What principal classes of these occur in protoplasm, and in what relative amounts? Which of them are electrolytes, and which are nonelectrolytes?
- 2. Review the chemical composition and molecular structure of carbohydrates. What are monosaccharides, disaccharides, and polysaccharides? Give examples of each. Review the chemical composition and molecular structure of fats. What general roles do lipids play in protoplasm?
- 3. What are proteins, and how are they constructed? In what ways do proteins differ from carbohydrates and fats? What is protein specificity? How is a coagulated protein different from a native or a denatured protein? Review the general biological roles of proteins.
- 4. What is the chemical composition and molecular structure of nucleoproteins? What are DNA and RNA? How are nucleotides related to DNA and RNA? What different kinds of nucleotides occur in protoplasm?
- 5. Define ionization, ion, electrolyte, acid, base, salt. Is KCN an acid, a base, or a salt? How does sodium sulfate (Na₂SO₄) ionize? The magnesium ion is Mg++, and the nitrate ion, already encountered in Chap. 5, is NO₃-; write the formulas for magnesium hydroxide, nitric acid, and magnesium nitrate.

- 6. What does the pH of a solution indicate? What would you expect the pH of a solution of NaCl to be? Of HCl? Of NaOH?
- 7. What is an enzyme, and how does it work? Why is invertase ineffective in accelerating the reaction glycerin + fatty acids → fat + water? What kind of enzyme does such a reaction actually require? Review the general operational characteristics of enzymes in protoplasmic reactions.
- 8. What is a colloidal system? How does such a system differ from a solution? What kinds of colloidal systems are possible, and what kinds occur in protoplasm? Review the properties of colloidal systems.
- 9. Define diffusion, and show how and under what conditions this process will occur. What is the biological significance of diffusion?
- 10. Define osmosis. Show how and under what conditions this process will occur. Distinguish carefully between osmosis and diffusion. Cite examples of biological situations characterized by isotonicity, hypertonicity, and hypotonicity.
- 11. What are the structural subdivisions of cells? What are the main components of each of these subdivisions, where are they found, and what functions do they carry out?

SUGGESTED COLLATERAL READINGS

Buswell, A. M. and W. H. Rodebush: Water, Sci. American, vol. 194, 1956.

Fruton, J. S.: Proteins, Sci. American, vol. 182, 1950. Linderstrom-Lang, K. U.: How Is a Protein Made? Sci. American, vol. 189, 1953.

Pauling, L., R. B. Corey, and R. Hayward: The Structure of Protein Molecules, Sci. American, vol. 191, 1954.

Pfeiffer, J. E.: Enzymes, Sci. American, vol. 179, 1948. Thompson, E. O.: The Insulin Molecule, Sci. American, vol. 192, 1955.

Vallee, B. L.: The Function of Trace Elements in Biology, Sci. Monthly, vol. 72, 1951.

CHAPTER 7

Monera and Protista

The preceding chapter has dealt with the organization of protoplasm and of cells; the three chapters now following deal with the organization of the larger living units made up of cells, namely, whole organisms. Just as the previous chapter has described the kinds of molecules in cells and their properties and structures, so now on this higher level we shall be concerned with the kinds of organisms and their structural and functional characteristics.

Organisms, like molecules, can be classified into types or categories. Thus, in studying the kinds of existing organisms, we direct our attention first to the methods and systems of classifying living creatures. With a frame of reference so established, we may then proceed with a systematic discussion of specific living types.

KINDS OF ORGANISMS

Methods of classification

Organisms are classified on the basis of their structure, function, development, and evolutionary history. The biological subscience which deals particularly with classification is called taxonomy.

The procedure of classifying organisms makes use of a universally recognized hierarchy of taxonomic ranks. In this hierarchy, any given rank usually contains several categories of lower ranks as components. Thus, if certain features are common to a large group of organisms, this group may be assigned a particular taxonomic rank. Within such a rank, several smaller groups of organisms can usually be distinguished on the basis of finer differences in features, and such smaller groups are then assigned the next lower rank. Each such lower-ranking group in turn may be subclassified further into a succession of progressively lower ranks.

Within the living world as a whole, the highest taxonomic rank usually recognized is the kingdom. By tradition going back several centuries, organisms are classified into two kingdoms, namely, the plant kingdom and the animal kingdom. It is highly questionable whether this tradition is still justifiable today, and there are good reasons to name kingdoms on a different basis. We shall further examine this point below.

The highest rank within a kingdom is the phylum; a kingdom contains several phyla. The phylum rank describes a broad grouping of historically usually closely related organisms, all characterized by the same structural and functional body organization. For example, all sponges, or all mollusks, as a group represent a phylum. Note that, strictly speaking, the name "phylum" is applied only to animal organisms; the equivalent term for plants is division. But for convenience, and because in certain instances the distinction between "plant" and "animal" is far from clear (see below), we shall use the term "phylum" uniformly throughout this book.

Within a phylum, the next highest rank is the class. For example, sponges may be subdivided into classes on the basis of their skeletons, one group having calcium skeletons, another silicon skeletons, and a third horny skeletons. Similarly, the phylum Chordata (all of which possess an internal skeleton, the notochord, at least as embryos) contains the class of mammals. These animals share the posses-

sion of a notochord with all other chordate classes, e.g., the birds, the reptiles, the fishes, and others (Chap. 9). But mammals are set off from all other classes by their possession of hair and by their nursing young with milk. Each other class has its own distinguishing features.

Using such criteria of likenesses and differences among and within groups, one may distinguish orders within a class, families within an order, genera within a family, and species within a genus. The species normally is the lowest unit. It is always identified by two technical names. For example, the species of grass frogs is known technically as Rana pipiens; the species to which we belong is called Homo sapiens. According to international rules, such species names are always underlined or printed in italics, and the first name must be capitalized. This first name always identifies the genus to which the species belongs. Thus the human species belongs to the genus Homo, and the species of grass frogs (as well as other frog species), to the genus Rana.

Sometimes it is desirable to make finer distinctions between two consecutive ranks. In that case an additional rank may be interpolated between the original two, and the prefix *sub-* or *super-* is then added to one of the main ranks. For example, between an order and a family, the order may contain several suborders, each suborder several superfamilies, and each of these, then, several families.

A complete classification of an organism tells a great deal about the nature of that organism. For example, suppose we knew nothing else about man except his taxonomic classification. Then we would know that he is characterized as follows:

Phylum Chordata, animals with notochords; subphylum Vertebrata, types possessing vertebral columns; superclass Tetrapoda, terrestrial animals with four limbs and bony skeletons; class Mammalia, forms with hair and milk glands; subclass Eutheria, animals in which the offspring develop within the body of the mother, with the aid of a nourishing and attaching organ called the *placenta*; order Primates, types with fingers instead of paws and flat nails instead of claws; family Hominidae,

animals with more or less upright posture, comparatively flat faces, stereoscopic vision, large brains, arms and legs, and hands and feet; genus *Homo*, forms with good chins, double-curved spines, long life spans, including long periods of youth, and forms which can laugh, weep, and in general display a great range of emotions; species *Homo sapiens*, forms with very erect posture, high foreheads, relatively thin skull bones, relatively short arms and long legs, and potentially high degrees of intelligence.

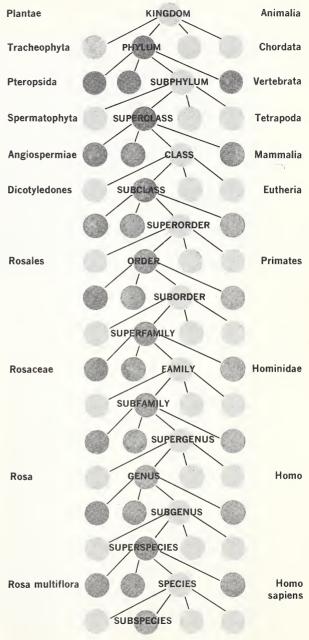
Even a brief taxonomic characterization such as this places an organism rather well, and we may note that a full, detailed classification would describe an organism completely. The taxonomic hierarchy and the classifications of a rose and of

man are diagramed in Fig. 7.1.

It may be pointed out that within a phylum, the member organisms often differ radically in their ways of life; consider, for example, the different ways of a fish and of man. Regardless of this, however, all organisms within a phylum use the same kinds of structures in solving the different problems of their different environments. Thus the fins of a fish and the arms of a man are basically the same kinds of structures; they both have evolved, along different paths, from one common ancestral type of body appendage.

In some cases it is not universally agreed whether a given group of organisms represents a distinct phylum, or a superphylum containing several smaller phyla, or a class within a larger phylum. Indeed, general agreement among biologists becomes better with the lower taxonomic ranks and worse with the higher ranks. The higher rank categories actually are being reshuffled more or less constantly, and this is probably as it should be. For these rankings incorporate the broad results of our knowledge of evolution, and as this knowledge improves, the rank categories must be adjusted

FIG. 7.1. The hierarchy of taxonomic categories. To serve as specific examples, the taxonomic classifications of a rose and of man are given to the left and right of the center diagram.



accordingly. A specific instance of such an adjustment will be discussed presently.

The main groups of organisms

In terms of the taxonomic system outlined above, what is the actual classification of specific large groups of organisms?

As noted earlier in passing, it is rather doubtful today whether the simple subdivision of the living world into plant and animal kingdoms is still adequate. For work during the past few decades has shown that certain groups of organisms really fit into neither the plant nor the animal category and should in fact be regarded as something else. At the same time, several other groups fit into both categories. For example, bacteria have very little in common with either plants or animals, and certain unicellular flagellate organisms can be regarded equally well as plants or as animals (see below).

A basic difficulty in this connection is that it is practically impossible to define "plant" or "animal" in adequate fashion. Every fundamental feature customarily used to define "plant" is encountered also among at least some "animals," and vice versa. To be sure, no one has any difficulty in deciding whether advanced organisms like trees or mammals are plants or animals. But such a difficulty does exist with primitive organisms, i.e., those closely related to the ancient ancestral types which gave rise to both trees and mammals. Such ancestral types possessed both plantlike and animal-like features simultaneously, and this is still true in their primitive descendants today. And if we go even further back in time, the very first organisms on earth probably possessed neither plantlike nor animal-like features at all, and this is again true for their present-day descendants.

The point is that plants and animals, clearly so recognizable, were not in existence right from the beginning. Rather, some of the early organisms evolved in plantlike and animal-like directions, slowly and gradually, and a definite, finalized "plant" status and "animal" status was attained only relatively late in evolutionary history. There-

fore a division of the living world merely into plant and animal kingdoms becomes too simple. It does not take this gradual development into account, and it allows no place for primitive organisms which are still neither "plant" nor "animal."

In view of this, attempts have been made in recent years to establish alternative classifications which do reflect our present knowledge of evolution. One such alternative scheme, in part already referred to in earlier chapters, recognizes not two but four basic categories of organisms: Monera, Protista, Metaphyta, and Metazoa. Each of these categories has a taxonomic rank roughly equivalent to a kingdom, although it may not be desirable to use this rank designation so long as it is technically still reserved for "plants" and "animals."

The identifying features and the phyla within the four categories will be discussed in detail in the sections and chapters which follow. Here we may note that the four groups are probably interrelated historically, as shown in Fig. 7.2 (see also Fig. 3.1). Every living creature has a proper place here. Monera and Protista include organisms which are plantlike, animal-like, neither, or both, as well as some of the organisms regarded as "true" plants (e.g., advanced algae) and "true" animals (e.g., most protozoa), and the Metaphyta and Metazoa include the remaining bulk of the "true" plants and animals.

Another point should be emphasized in this context. All available evidence indicates that living evolution has the general pattern of a greatly branching bush. All presently living organisms are contemporaries, appearing at the uppermost branch tips of the bush. Ancestral types, mostly long extinct, appear lower down on the bush, where branches join. Thus a given common ancestory may give rise to several different types of descendants, each inheriting the characteristics of the common ancestor and evolving innovations of its own. And a particular descendant living today may become a common ancestor of new and different types living tomorrow.

A corollary of the above is that the pattern of evolution is *not* that of a "ladder" or a "scale."

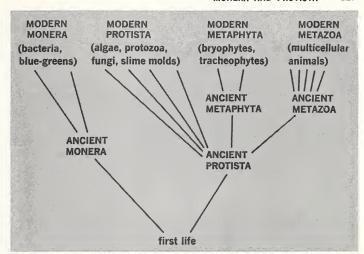


FIG. 7.2. The main groups of organisms and their probable evolutionary relationships. Note the bush pattern of evolution.

Many uninformed people still speak of a "scale of evolution," implying a straight-line progression from one organism directly to the next, usually from some "low" type like a protozoan ameba to some "high" type like a metazoan man. Such statements testify only to ignorance, human vanity, or both, not to actual biological knowledge. For a glance at Fig. 7.2 will show that there simply is no straight-line "scale," but a branching pattern. Moreover, neither man nor the ameba is descended from the other, but both are modern contemporaries and have evolved coequally and along entirely separate paths, from some ancient, long extinct protistan common ancestor. Finally, among currently living organisms, there simply are no "higher" and "lower" types, since all place equally high (or equally low) on the evolutionary bush. There are only different types, with different histories and different characteristics. Note, incidentally, that the above holds true just as completely if instead of interrelating amebae and man we interrelate monkeys and man.

The remainder of this chapter will deal with the characteristics of the various moneran and protistan

groups. Metaphyta and Metazoa will be examined in the two following chapters.

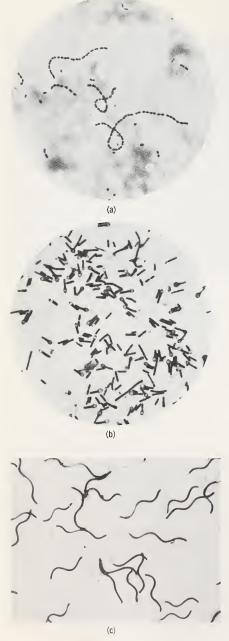
THE MONERA

These organisms are distinguished from all other forms of life in that they do not possess a true cell nucleus. The gene-containing nucleoproteins here are clumped together more or less in the center of the cell, but there is no surrounding membrane and the nucleoproteins are in direct contact with the rest of the cell substance. As noted in Chap. 2, this is also believed to have been the internal organization of some of the earliest cells on earth. These cells may have been directly ancestral to the present Monera.

The Monera are all basically unicellular, but in some cases the cells are aggregated together into colonies and other multicellular masses. Two phyla are included in the group, the *bacteria* and the *blue-green algae*.

Phylum SCHIZOPHYTA: bacteria (2,500 species)

As a group, bacteria represent the smallest cells now in existence. The tiniest of them are smaller



even than certain gigantic viruses, and the largest are not substantially larger than very small cells of other organisms. Bacteria usually possess a cell wall, made of a chitinlike material or of complex polysaccharides. Many bacteria occur as single cells, but many others grow in clumps, forming chains, plates, or compact aggregates. Many also possess exceedingly fine surface filaments which endow them with a certain amount of self-powered mobility. On the basis of shape, three kinds of bacteria may be distinguished. A coccus is a spherical type, a bacillus a rod-shaped type, and a spirillum a coiled type (Fig. 7.3).

Some bacteria are chemosynthesizers or photosynthesizers, and these produce their own food. The photosynthesizing types possess a unique variety of chlorophyll called bacteriochlorophyll. These forms do not possess chloroplasts. Instead, the bacteriochlorophyll is located in tiny granules dispersed throughout the cytoplasm. Bioluminescence is fairly common within the phylum.

Most bacteria depend on other organisms for food. Of these, some are free-living saprophytes in soil or ocean, and the rest are parasitic, commensalistic, or mutualistic symbionts. Also, some bacteria must have oxygen for respiration, others can do without it and respire by fermentation, and still others may survive both with and without oxygen. In most of these types, reserve foods are stored in the form of the polysaccharide glycogen (as in man).

Bacteria reproduce by cell division. This is an enormously effective process, for under good conditions bacterial cells may divide every 20 min or so. Thus a single bacterium may, in just 6 to 7 hr, produce 1 million offspring! It may be easily appreciated, therefore, that bacteria probably outnumber all other living organisms on earth. On occasion, certain bacteria may secrete heavy walls around themselves and are then known as "resting spores." In this state they may survive unfavorable condi-

FIG. 7.3. Bacteria. (a) Cocci, growing in chains. (b) Bacilli. (c) Spirilla. (General Biological Supply House, Inc.)

tions. It has been discovered recently also that some bacteria may mate and undergo a sexual process. This subject will be discussed further in Chap. 20.

Three groups of bacteria are of major significance to all other life on earth: those which, in soil and ocean, bring about *decay*; those which are *nitrogenfixing*, *nitrifying*, and *denitrifying* and so provide nitrogen usable by other organisms and generally maintain the global nitrogen cycle (Chap. 5); and those parasitic bacteria which produce disease, the *pathogenic* bacteria. Note here that certain bacteria probably also cause diseases indirectly, by releasing pieces of their nucleoprotein clumps as viruses (Chap. 2).

Evidently, the phylum is highly diversified. In spite of the exceedingly small size of the individual bacterium, there is certainly nothing "simple" about it. Its molecular and chemical complexity is quite as great as that of any other cell type, and it often lives in a way and in an environment in which few other organisms can. Indeed, if man is challenged in his dominance by anything living, his greatest challenger is probably the bacterium.

Phylum CYANOPHYTA: blue-green algae (2,500 species)

This phylum name is somewhat misleading, since the designated organisms probably are not true "algae." They appear to be rather more closely related to the bacteria. The name "algae" here is a holdover from classifications in which blue-greens and true algae all are considered to be members of the "plant kingdom." Furthermore, the blue-green algae are not actually blue-green, but are of red, yellow, green, blue, and various intermediate shades. These colors are produced by several pigments. A variety of chlorophyll called chlorophyll a is usually always present, and in addition there are other colored substances, including a blue phycocyanin and a red phycoerythrin pigment. The last two are quite unique to the phylum, occurring in no other.

Like bacteria, the cyanophytes are fundamentally single cells, very small, and equipped with cell walls composed in part of cellulose (Fig. 7.4). Like

Gloeocapsa

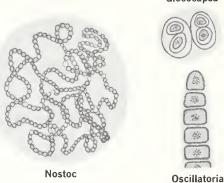


FIG. 7.4. A variety of blue-green algae.

bacteria also, they lack a nuclear membrane internally. Like photosynthetic bacteria, the cyanophytes do not possess chloroplasts. Instead, chlorophyll is in granules dispersed through the cytoplasm.

Some cyanophytes are known which do not possess chlorophyll, having apparently lost photosynthetic capacity during their evolution. It is exceedingly difficult to distinguish such organisms from colorless bacteria. Again like certain bacteria, many cyanophytes may fix molecular nitrogen from the atmosphere and many are bioluminescent. Food is stored in the form of a unique type of starch, called cyanophycean starch.

Most blue-greens are fresh-water forms, but some are marine. The organisms characteristically grow in colonial filaments, often greatly branched, or in clumps of various shapes. In many cases, such colonies are embedded in a gelatinous material secreted by the cells. The blue-greens reproduce by cell division, like bacteria. Sexual processes are entirely unknown in this phylum.

THE PROTISTA

This group includes an enormous assemblage of types, all believed to be more or less direct descendants of very early cells which had evolved a true cell nucleus, with a membrane separating the genecontaining nucleoproteins from the cytoplasm. In addition, the protistan ancestors probably developed several other evolutionary "inventions," and these too are characteristic of the modern Protista.

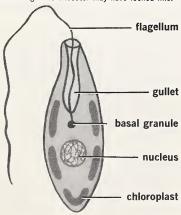
First, early Protista probably featured whiplike flagella projecting from their surfaces, structures which could be used in locomotion. Under certain conditions the flagella probably could be cast off, and the cells could then propel themselves by ameboid locomotion. Flagella could then be regrown. In primitive modern Protista too, a flagellate condition is typical, one or more flagella being present sometimes throughout life, sometimes at certain stages only (Fig. 7.5). In many cases, moreover, the flagella may be shed and ameboid movement may be undertaken.

Second, the gene-containing nucleoproteins within the nucleus of the Protista are not in clumps as in the Monera, but occur in the form of clearly identifiable chromosomes.

Third, outside the nucleus there is typically a centriole (largely lost in the Metaphyta, but retained in the Metazoa).

Fourth, a new method of cell division is in evi-

FIG. 7.5. The basic structure of a flagellate, suggesting what the first protistan flagellate ancestor may have looked like.



dence. This method is **mitosis**, about which more will be said in Chap. 19. Note here that mitosis depends on the presence of chromosomes and does not occur in the Monera.

Fifth, ancestral Protista probably could supply themselves with nutrients either by photosynthesis, or by saprophytism, or by symbiosis, or by eating. Some modern Protista still retain this multiplicity of choices. Others have concentrated on one of these methods and have lost the others.

Sixth, ancestral protists probably "invented" chloroplasts, not present in the Monera. Chloroplasts are still characteristic of all modern photosynthetic Protista, as well as all Metaphyta.

Seventh, the unicellular condition of the protistan ancestors is still basic for most living Protista, but some groups have independently evolved an often highly advanced degree of multicellularity.

These fundamental features identify all living Protista, and almost all are characteristic also of Metaphyta and Metazoa. It is for this reason that the last two groups are believed to have evolved from the first.

Protista today include the various true algae, the fungi, the slime molds, as well as the various protozoa.

Algae

As a group, algae may be regarded as a superphylum containing several distinct phyla. Primitive living algae are still unicellular, flagellate, and both plantlike and animal-like in their nutrition. But more advanced algae are multicellular, sessile, and able only to photosynthesize.

The algal phyla are distinguished primarily by biochemical features: types of chlorophyll and other pigments present, chemical composition of the cell wall, the chemical nature of the stored food (Table 5). Secondarily, structural distinctions are useful also.

On the basis of their chlorophyll content, three major subcategories of algae may be recognized. *All* photosynthesizing algae possess the variant of chlorophyll called chlorophyll *a*. In this respect

TABLE 5. Comparative biochemical characteristics of various plant groups*

Group	Chlorophyll	Other pigments	Food stored as:	Cell wall contains:
Cyanophyta	a	Phycocyanin, phycoerythrin (both unique)	Cyanophycean starch (unique)	Cellulose
Chlorophyta Bryophyta Tracheophyta	a, b		Starch	Cellulose
Dinoflagellata	a, c	Fucoxanthin		Cellulose in some; others no wall
Chrysophyta	a, c	Fucoxanthin	Oils	Silica
Phaeophyta	a, c	Fucoxanthin, unique xanthophylls	Mannitol, laminarin	Cellulose
Rhodophyta	a, d	Phycocyanin, phycoerythrin (both unique)	Floridean starch (unique)	Cellulose

^{*} Most groups contain a variety of common carotene and xanthophyll pigments, which are not specially indicated in the table.

algae are like the cyanophytes of the Monera, and chlorophyll a may represent an inheritance from the very earliest cells, shared alike by Monera and Protista. But the protistan algae developed other variants of chlorophyll too, and at least one of these others is always present in addition to chlorophyll a. Thus one major group of algae possesses chlorophylls a and b. This group may be called the green-line stock, for the two chlorophylls and the other pigments present in these organisms together produce a color which is some shade of green. A second major algal group possesses chlorophylls a and c. This group may be called the brown-line stock, for analogous reasons. A third group possesses chlorophylls a and d, and it constitutes a red-line stock.

The green-line algae

Phylum CHLOROPHYTA: green algae (5,000 species)

Class Chlorophyceae: green algae proper Chlamydomonas, Polytoma, Volvox, Spirogyra, Ulva, Acetabularia Class Charophyceae: stoneworts

Chara, Nitella

The primitive members of this phylum are flagellate unicells. In many of these, the flagella may disappear at certain stages of the life cycle, and the organisms then may move like amebae. Other green algae are colonial, and in forms like *Volvox*, for example, the cells are interdependent to a substantial degree (Fig. 7.6). Still other green algae are truly multicellular (e.g., the "sea lettuce" *Ulva*, Fig. 7.7).

Many of the unicellular green algae include, on the one hand, types which photosynthesize and, on the other, strikingly resembling types which are colorless and live as saprophytes. For example, Chlamydomonas is a green photosynthesizer, and Polytoma is a colorless nonphotosynthetic form exceedingly similar to Chlamydomonas in all other respects (Fig. 7.8). As we shall see, paired types of this sort are encountered also among the other algal phyla. Such paired types undoubtedly represent branch lines from a relatively recent common ancestor, one line having retained, the other lost, the photosynthetic method of nutrition. Indeed, in certain cases experiments may duplicate such evolutionary processes. For example, it has been possible to convert certain photosynthetic algae into variant

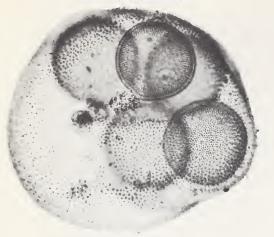


FIG. 7.6. Volvox, a colonial green alga consisting of many flagellate cells. The cells are arranged as a single-layered sphere, with each cell in direct contact with the water environment. In the interior of the sphere are several offspring colonies, which develop there and eventually burst through the parent. (General Biological Supply House, Inc.)

strains which lack chlorophyll and photosynthetic capacity. Such animal-like variants thrive perfectly well if a ready-made source of foods is supplied them from the outside. Very probably, experiments of this sort also simulate the ancient natural process by which original flagellate stocks may have given rise separately to plantlike and animal-like organisms.

Green algae today are exceedingly widespread and are found wherever there is water. Most are small and microscopic, especially the unicellular types. However, certain of the single-celled varieties may attain considerable size. A famous example is *Acetabularia*, found in warm seas. The alga is 2 to 4 in. long and consists of a stalk tipped by an umbrellalike cap. The whole is a single cell, and a single nucleus is present in the stalk (Fig. 7.7).

Structurally, probably the most complicated green algae are the stoneworts, usually found in fresh-

FIG. 7.7. Three types of green algae (diagrammatic).

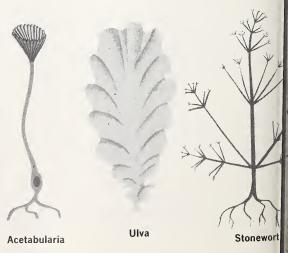
water ponds. These multicellular algae resemble miniature trees, with whorls of leaflike branches attached at more or less regular intervals to a stemlike stalk. This stalk is anchored to the ground by rootlike processes (Fig. 7.7). As a group, the stoneworts may represent an evolutionary experiment in advancing the basic algal organization in a direction actually taken later by terrestrial plants.

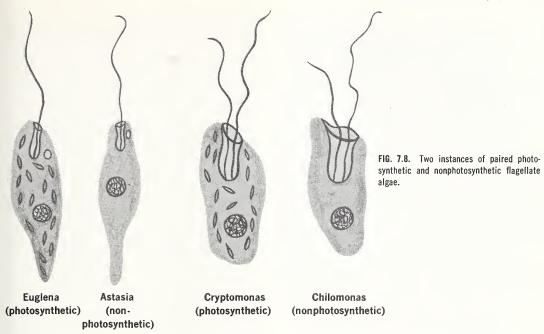
In addition to chlorophylls *a* and *b*, all green algae typically possess pigments called **carotenes** and **xanthophylls**. The principal food-storage compound is starch. Cell walls typically are composed of cellulose, at least in part. Taken together, these various chemical characteristics are very distinctive, and among all other living organisms they occur in precisely this combination only in the Metaphyta (Table 5). For this reason, the Metaphyta are believed to have evolved from an early group of the green algae.

Phylum EUGLENOPHYTA

Euglena, Astasia

This relatively small group belongs to the greenline stock of algae too, but the organisms differ in several respects from the chlorophytes. Thus euglenophytes are exclusively unicellular and permanently flagellate; they store fatty materials, not





starch; their body is without rigid cell walls and therefore pliable; and they have a distinct internal cell structure (as regards, for example, the number of chloroplasts present). Many also possess an "eyespot," a pigment granule sensitive to light and probably used in orientation to light.

Here too we find paired types of green and colorless forms. For example, *Euglena* is a green photosynthesizer, interesting also in that it can, and probably must, occasionally feed as a saprophyte, regardless of whether or not light is present. *Astasia*, on the other hand, is a colorless saprophyte, otherwise entirely similar to *Euglena* (Fig. 7.8).

The brown-line algae

Phylum CHRYSOPHYTA: golden-brown algae Class Chrysophyceae: yellow-brown algae Class Xanthophyceae: yellow-green algae Class Diatomeae: diatoms These organisms are primarily, but not exclusively, unicellular or colonial forms. They are identified by chlorophylls *a* and *c* and by various carotene and xanthophyll pigments, the latter including the conspicuous yellow-brown pigment fucoxanthin. Foods are stored mainly in the form of oils, and starch is never present. Cell walls usually occur, characterized by the presence of silicon compounds.

Chrysophytes typically possess permanent flagella (but diatoms have flagella only at certain stages). The class Chrysophyceae very probably includes the most primitive members of the phylum, and here again we find many photosynthetic and colorless paired types. The yellow-brown class is an exceedingly diversified group generally, including types with different numbers of flagella, types which may lose flagella altogether and then behave like amebae, and types with a wide array of different surface structures and configurations. Partly because

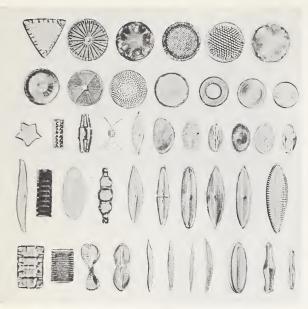
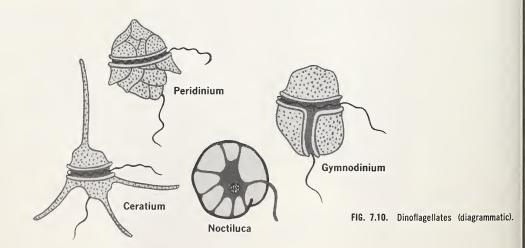


FIG. 7.9. An array of diatoms. See also Fig. 5.2. (General Biological Supply House, Inc.)

of this diversification, it is thought that early Chrysophyceae may have been exceedingly rich in evolutionary descendants. Indeed, they may well have been the ancestors of the whole present collection of brown-line phyla; and, via loss of chlorophyll, they may also have given rise to various protozoa and conceivably even to some of the Metazoa. If this can be substantiated, early yellowbrown algae might turn out to relate to the Metazoa just as early green algae are more surely suspected to relate to the Metaphyta.

Apart from this possible ancestral significance, chrysophytes other than diatoms have relatively little importance in the economy of nature. But the diatoms more than make up for this. As already pointed out in Chap. 5, diatoms are the most abundant single group of plankton organisms, and as such they support much of the flora and fauna of the oceans and the fresh water (Fig. 7.9; also Fig. 5.2). We may note that the silica shells of dead diatoms make up large tracts of the ocean floor and that geologically uplifted parts of this floor are the source of diatomaceous earth, mined for its abrasive properties. We may note too that much of the



petroleum used in industry today is probably derived from the oils synthesized by diatoms of past ages.

Phylum PYRROPHYTA

Class Cryptomonadina

Cryptomonas, Chilomonas

Class Dinoflagellata

Noctiluca, Ceratium, Gymnodinium, Blastodinium, Peridinium

These organisms (Figs. 7.8 and 7.10) are almost exclusively unicellular and flagellate. The group is distinguished by possession of chlorophylls a and c, the pigment fucoxanthin, and the presence of cell walls made of a celluloselike material.

As in the other algal phyla already described, both classes of the pyrrophytes contain types with different nutrition. Among the dinoflagellates, for example, *Ceratium* is photosynthetic, *Blastodinium* is parasitic in animals, and *Noctiluca* both photosynthesizes and may feed like a free-living animal. Closely related pairs of types with different nutrition are also known in this class. And among the Cryptomonadina, *Cryptomonas* and *Chilomonas* represent a photosynthetic-nonphotosynthetic pair (Fig. 7.8).

Most free-living dinoflagellates are marine and form a major component of plankton (Fig. 7.10). One group, which includes *Peridinium* and *Ceratium*, is characterized by the presence of an external celluloselike armor, consisting of two or more interlocking plates. These organisms are encircled by a groove which shelters one of the two locomotor flagella. Many marine dinoflagellates are bioluminescent (e.g., *Noctiluca*), and some on occasion proliferate locally in fantastic numbers. For example, the reddish *Gymnodinium* often produces so-called "red tides" (hence the name of the phylum, which literally means "fire plants").

Phylum PHAEOPHYTA: brown algae (1,000 species)

Chlorophylls a and c and the pigment fucoxan-thin are again characteristic of the phylum. Food is stored either as mannitol, an alcohol formed from the sugar mannose, or as laminarin, a unique polysaccharide formed from glucose and found only



FIG. 7.11. A portion of Fucus, a common brown alga found attached to rocks on the seashore. Note the air bladders along the leaflike body. The bulbous parts at the ends of the body contain reproductive structures. (General Biological Supply House, Inc.)

in these algae. The cell walls contain cellulose.

Brown algae living today apparently do not include any primitive representatives, for they are exclusively multicellular. The largest of all algae belong to this phylum. Flagellated cells occur only at certain stages of the life cycle. Brown algae are almost entirely marine and include most of the seaweeds. The majority of species are found in shallow water and in the tide zone, where they are



FIG. 7.12. The red alga Polysiphonia. Note the delicate, lacy structure. (General Biological Supply House, Inc.)

attached to rocky bottoms by holdfasts. Ebb tides may expose them to the air for periods of several hours. The most familiar of the brown algae is probably the rockweed *Fucus*, found along many shores (Fig. 7.11). Undoubtedly the most spectacular of the seaweeds are the kelps. For example, the giant kelp *Macrocystis* sometimes attains lengths of

more than 100 yd, which makes it longer than a full-grown blue whale. *Laminaria* is the commonest of the kelps. Torn pieces of it may usually be found washed up on beaches, particularly after a storm.

The red-line algae

Phylum RHODOPHYTA: red algae (3,000 species)

This phylum is characterized by the possession of chlorophylls a and d and variants of the pigments phycocyanin and phycoerythrin. The last two are of unique composition and are chemically not the same as the pigments of like name in the bluegreen algae. Red algae store food in the form of floridean starch, chemically distinct from the common starch found in green algae. The cell walls are of cellulose.

Red algae are exclusively multicellular and almost exclusively marine (Fig. 7.12). They live in somewhat deeper water than the brown algae, and their red pigment phycoerythrin appears to be an adaptation to their dimmer environment. For phycoerythrin absorbs blue light particularly well, and the "blue" wavelengths of sunlight actually penetrate deeper into water than "red" wavelengths. Indeed, phycoerythrin has been found to play an important auxiliary role in the photosynthesis of these algae. Red algae are lacier and more delicate than the sturdy brown algae. The latter are adapted to withstand pounding surf, but in deeper water the red algae are not so subject to wave action.

Some of the red algae are used commercially. The genus *Gelidium* is the source of agar jelly, and *Porphyra*, *Rhodymenia*, and *Chondrus crispus*, the Irish moss, are among several types prized as vegetables in various parts of the world.

Rhodophytes as a whole are a relatively advanced group. They are not obviously related to any of the other algal phyla, and they must have evolved, in ways unknown to us, from early ancestral unicellular stocks. Indeed, the problem of relating this phylum is particularly difficult, for in the entire group there is not a single organism, or cell type, or life-cycle stage which exhibits even one flagellum

or cilium. This total absence of flagella is quite unique among Protista and suggests an interesting, though still unknown, evolutionary origin of the group.

Protozoa

Classified traditionally as a single phylum of "animals," these organisms are best regarded as a superphylum within the Protista. The unicellular condition is almost universal, but some protozoa form colonies. And although all protozoa are colorless and nonphotosynthetic, there is excellent reason to think that they all arose, directly or indirectly, from photosynthetic ancestors. Indeed, the ancestral source of protozoa was probably quite varied. Flagellate or ciliate protozoa might have evolved directly from some of the earliest flagellate stocks which also gave rise to the algae. Or certain later flagellate algae might have lost chlorophyll and so have evolved into protozoa. Or ameboid types might have lost chlorophyll and become protozoa in this fashion. All these different sources, and others as well, probably contributed to what we now recognize as protozoa.

Protozoan stocks have exploited the unicellular, nonphotosynthetic way of life. They are either parasites or free-living animal-like eaters, and they feature a tremendous array of varied internal specializations. There is usually a surface cuticle or secreted shell, and various protrusions project from the cell surface: flagella, or cilia, or modifications of these, or flowing "fingers" of protoplasm called pseudopods. As in other organisms, these structures serve variously in locomotion, in feeding, or in the creation of water currents. In most protozoa, deep pits at given points of the cell surface are specialized as mouths and gullets, and many others engulf solid food by means of pseudopods. Internally, given species of protozoa may possess up to several hundred nuclei.

The number of existing protozoan species has been underestimated fairly consistently. Figures often quoted are in the order of 15,000, but there are known to be more than that many foraminiferan species alone. Moreover, most animals usually harbor at least one parasitic protozoan species, which means that protozoa could well number in the hundreds of thousands of species. As a conservative figure, at least 100,000 species of protozoa may be presumed to exist.

Protozoa are classified into phyla according to their methods of locomotion.

Phylum MASTIGOPHORA: zooflagellates
Trypanosoma, Proterospongia, Trichonympha,
Trichomonas

The ancestors of this group undoubtedly were close kin to the early photosynthesizing flagellates which gave rise to the algae. After losing chlorophyll, these colorless flagellates evolved in their own way in rather animal-like fashion. Some remained free-living bulk feeders, others became saprophytes, and still others adopted various symbiotic ways of life. Parasitic forms are particularly common today. Among the free-living types are *Proterospongia*, the so-called collar flagellates, which feed on debris and

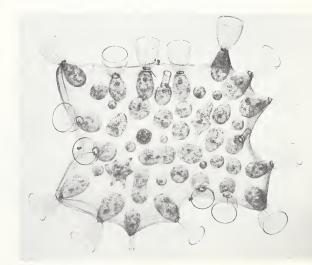


FIG. 7.13. The colonial zooflagellate Proterospongia. These cells are embedded in secreted jelly. Photo of glass model. (American Museum of Natural History.)

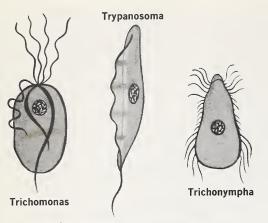


FIG. 7.14. Three types of zooflagellates (diagrammatic).

minute organisms. Food is trapped within the collar of these cells, and the flagellum then creates a current which sweeps the food toward the cell body, where it is engulfed (Fig. 7.13). Among the parasitic types are *Trypanosoma*, different species of which live in the bloods of various vertebrates. One such

species causes sleeping sickness in man. *Trichonympha* is a mutualistic wood-digesting symbiont in the gut of termites, and *Trichomonas* is a commensal in the gut of man and other vertebrates (Fig. 7.14).

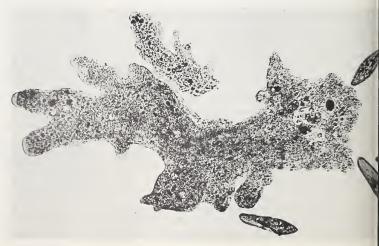
The ancestors of the modern zooflagellates are believed to have been one of the sources from which other protozoan phyla may have evolved.

Phylum SARCODINA: amebae, foraminifera, radiolaria

These protists move and feed by means of pseudopods. Some, like the various species of *Amoeba* (Fig. 7.15; also Fig. 3.5), are naked cells, and these include a good many parasitic forms. For example, *Entamoeba histolytica* causes amebic dysentery in man.

Other sarcodines enclose their bodies in secreted shells. A chitinous housing is present in *Arcella*, the organism extruding pseudopods through an opening in the shell. *Difflugia* cements tiny sand particles to a chitinous envelope (Fig. 7.16). The foraminifera manufacture calcareous shells of many different forms, all resembling tiny snail shells (Fig. 7.17). Pseudopods are extruded through holes in these shells, hence the name "foraminifera," which

FIG. 7.15. The large organism is Pelomyxa, a multinucleate sarcodine protozoon related to the common ameba. Such a common ameba is shown just above Pelomyxa. In both, note the pseudopods, which trap food. Some paramecia are shown on the right; these ciliate protozoa are favorite food organisms of Pelomyxa. (Carolina Biological Supply Co.)



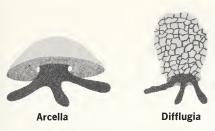


FIG. 7.16. Two kinds of sarcodine protozoa (diagrammatic).

means "hole bearers." Foraminiferan shells may accumulate in given tracts of ocean floor in such numbers that they form the predominant bottom deposit in such regions. This is true also of radiolarian shells, which consist of silica (Fig. 7.17). Foraminiferan deposits may become transformed into chalk, radiolarian deposits into flint. When either of these is uplifted geologically, they may contribute massively to the formation of land (e.g., the chalk cliffs of Dover).

Phylum CILIOPHORA

Class Ciliata

Paramecium, Stentor, Euplotes, Vorticella Class Suctoria

Podophrya, Tokophrya

These protozoa (Fig. 7.18; also Fig. 6.17) move and feed by means of cilia, arranged in most species into orderly rows. The phylum is characterized also by the presence of two kinds of nuclei in each organism. The so-called micronucleus functions principally in sexual processes, and the macronucleus controls metabolism, development, and most other cellular processes. Several of both kinds of nuclei may be present in a single organism. This unique nuclear specialization is paralleled by a very high degree of cytoplasmic specialization. For example, ciliates typically possess permanent mouths, excretory vacuoles, contractile fibrils, neural fibrils, holdfasts, and locomotor apparatus.

Some ciliates are colonial and sessile, and many are parasitic. The class Suctoria comprises forms

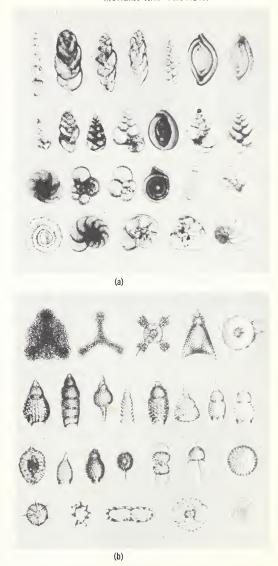


FIG. 7.17. (a) Foraminifera; (b) radiolaria. The shells of the former are made of calcium salts, those of the latter of silicon compounds. (General Biological Supply House, Inc.)

136

FIG. 7.18. Various ciliophorans. The photo shows Paramecium, stained to reveal the macronucleus (large dark central body) and the micronucleus (small dark body partly overlapping the macronucleus on the top). Another ciliate is shown in Fig. 6.17. (Photo, Carolina Biological Supply Co.)



which are ciliated and free-swimming only during young stages. Adults are sessile and unciliated, and they feed by means of tentaclelike protrusions which capture and suck up the protoplasm of other protozoa.

Phylum SPOROZOA

Plasmodium

All sporozoa are parasitic. They are characterized by wholly passive locomotion and by very complex life cycles which often involve multiple hosts. The most familiar genus is undoubtedly *Plasmodium*, various species of which cause malaria in man and other mammals and in birds. In human malaria, the *Anopheles* mosquito is the specific intermediate host of the protozoan parasite (Fig. 7.19).

Slime molds

Phylum MYXOPHYTA

Vorticella

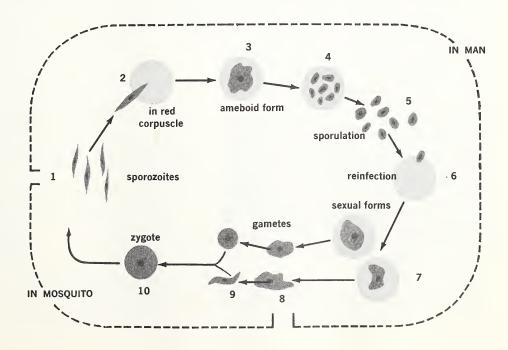
These interesting nonphotosynthetic organisms share certain characteristics with ameboid protozoa, others with fungi. In traditional classifications, slime molds are actually grouped sometimes with the "animal kingdom," sometimes with the "plant kingdom." Like protozoa and fungi, slime molds are without chlorophyll, and their exact origin among protistan ancestors is obscure.

The life cycle of slime molds reveals both their protozoalike and funguslike features (Fig. 7.20). In an initial stage, the organisms exist as solitary flagellate cells, greatly resembling the animal-like zooflagellates. These solitary cells reproduce by cell division. At a later stage, the cells fuse pairwise, lose the flagella, and become strikingly amebalike in locomotion and feeding behavior. Still later, ameboid cells which come into contact with one another clump together, and in many species the cell membranes dissolve in addition (Fig. 7.20). The result is a huge colonial or continuous mass of protoplasm, in some cases as much as I ft or more in diameter. Up to this point the life cycle is rather protozoalike. A funguslike phase then supervenes. From the protoplasmic mass grow out one or more upright stalks, and the tips of these expand into fruiting bodies. Within them, numerous spore cells are formed, each containing one nucleus and a hard shell on the outside. The spores eventually scatter, and in suitable environments they may germinate and develop into solitary flagellate cells. These begin a new cycle.

Fungi

Modern fungi all are either saprophytic or symbiotic, and none is green. They too probably arose from early flagellate stocks, via loss of chlorophyll. Today they are almost exclusively multicellular,

FIG. 7.19. The life cycle of the sporozoan malarial parasite Plasmodium. The organism is injected by an Anopheles mosquito into the human blood stream in the form of flagellate sporozoite cells (1). Sporozoites enter red corpuscles, transform into ameboid cells, and undergo multiple fission (2) to (4). The corpuscles then rupture and release the ameboid cells, a process accompanied by a characteristic attack of fever. Ameboid cells then may reinfect other red corpuscles, undergo fission, and by repeated reinfections bring about repeated fever cycles (5), (6). Some of the ameboid cells eventually transform into gamete producers (7), (8), and these are sucked up by a mosquito, along with blood. In the gut of the mosquito gametes form, fertilization occurs, and the ameboid zygote penetrates through the gut wall into the blood of the insect (9), (10). Here the zygote encysts, undergoes multiple fission, and forms many flagellate sporozoites. These escape from the cyst, find their way into the salivary glands of the mosquito, and are then injected into human blood when the insect bites man.



2 solitary ameboid cells

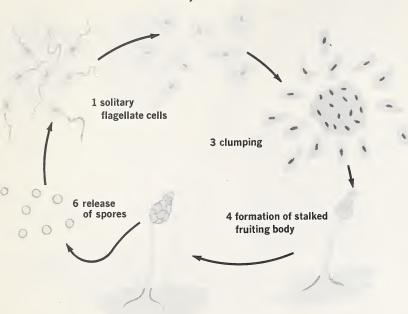
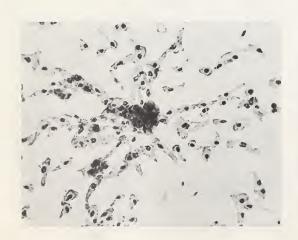


FIG. 7.20. Slime molds. The diagram shows the typical life cycle. Note the animal-like and plantlike phases. The photo shows the migrating ameboid cells, which aggregate into a compact mass and later develop into a fruiting body. (Photo, Dr. J. T. Bonner, "J. Exptl. Zool.," vol. 106, p. 7.)

5 spore production in fruiting body



and they are exceedingly common in all environments which contain organic materials. Virtually all other protists are aquatic, but fungi are largely terrestrial. The decay- and disease-causing activities of these organisms make them a group of major importance.

Phylum MYCOPHYTA: fungi (90,000 species)
Class Phycomycetes: tubular fungi

Bread molds

Rhizopus

Water molds

Saprolegnia

Downy mildews, blights, white rusts

Class Ascomycetes: sac fungi

Molds

Neurospora, Penicillium

Yeasts

Saccharomyces

Powdery mildews, truffles, lichens

Class Basidiomycetes: club fungi

Mushrooms, toadstools, rusts, smuts, bracket fungi, puffballs, lichens

Class Fungi Imperfecti

A heterogeneous collection of types which, because of unknown reproductive patterns, cannot yet be assigned to any of the other three classes

The basic unit of fungus structure is a hypha, a tubular, multinucleate filament which may be branched. A mass of meshed hyphae forms a mycelium, and this constitutes the main body of a fungus. Mycelia may be underground, but growing from them are spore-forming fruiting bodies of varied construction, and these are the exposed parts of the fungi.

The class Phycomycetes is probably the most primitive of the phylum. Some members of these ubular fungi are unicellular, but most are multinucleate syncytia, like the common bread mold *Rhizopus*, which forms white fuzzy growths on stale pread (Fig. 7.21).

The sac fungi are so called because their spores are manufactured in sacs, or asci. Such asci are often located in cup-shaped fruiting bodies (Fig. 7.22). The hyphae of ascomycetes may become thick

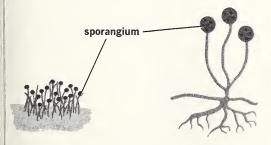


FIG. 7.21. Diagram of the spore-producing structures (fruiting bodies, or sporangia) of the bread mold Rhizopus (whole view and detail). Stalked spore cases as shown are farily typical of phycomycete fungi generally.



FIG. 7.22. Ascomycetes. (a) Section through a cup fungus, showing layer of asci just under inner surface of cup. (b) Detail of layer of asci. Note the spores in each ascus. (G. H. Conant, Triarch Products.)

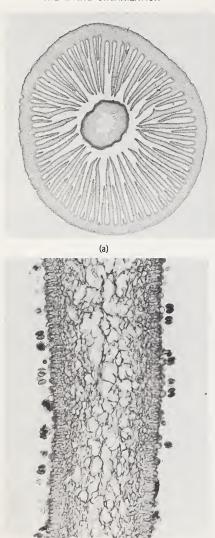


FIG. 7.23. (a) Section through the cap of a mushroom, showing the arrangement of the gills. (b) Close-up of a gill. Note the mycelial meshwork in the interior and the spores attached to basidia and projecting from the surface. (General Biological Supply House, Inc.)

and fleshy, as in truffles. Some of the ascomycetes are unicellular, like the yeasts. Sac fungi produce many diseases, while some, like *Penicillium*, are sources of antibiotics which will cure disease. Ascomycete molds also produce the characteristic flavor of Roquefort, Camembert, and other kinds of cheeses. Symbiotic combinations of fungi and algae form lichens. The fungal members of these grayish and yellowish rock-encrusting combinations in most cases are ascomycetes, and the photosynthetic members, blue-green and green algae.

The Basidiomycetes are believed to have evolved from the Ascomycetes, and they are structurally the most complex of all the fungi. They are characterized by a specialized spore-producing unit, the basidium. This is an enlarged, club-shaped, terminal cell of a hypha. Many basidium-bearing hyphae may be combined into a large, stalked fruiting body, familiarly known as a mushroom. In many cases, the cap of a mushroom has radially arranged plates on its underside, called gills. On these, the spore-bearing basidia are exposed to the external environment (Fig. 7.23).

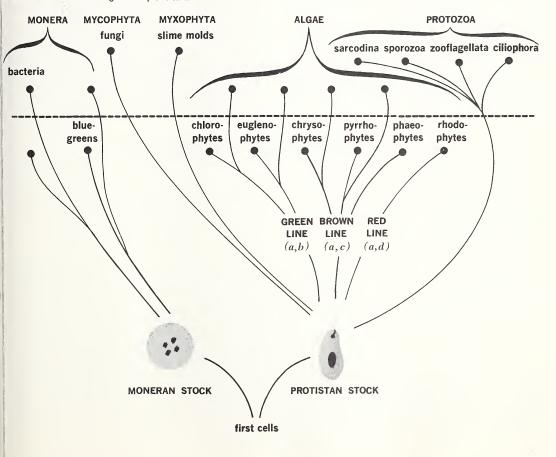
Not all basidiomycetes form mushrooms, however. Among those which do not may be mentioned specially the *puffballs* and *stinkhorns*. In these, the basidia are not exposed to the air, as in mushrooms, but are initially embedded within the fruiting body. This body eventually breaks open, and the mass of spores is then extruded. Giant puffballs are known to reach diameters of about 5 yd, and they probably have the distinction of being reproductively the most prolific organisms of all. A single giant puffball may manufacture as many as 100 *trillion* spores. It has been estimated that if each of these were to grow into a mature fungus, a mass of tissue close to 1,000 times the size of the earth would be produced.

The above accounts of the Monera and the Protista show that these organisms are exceedingly varied and of vital significance in the overall economy of life on earth. In this connection it may be kept in mind that Monera and Protista were the

only living creatures present during most of the time in which life existed on earth. The popularly more familiar Metaphyta and Metazoa are relatively late products of evolution.

The probable interrelations of the various moneran and protistan groups are shown in Fig. 7.24 below.

FIG. 7.24. The probable interrelations of the various main groups within the Monera and the Protista. The horizontal line separates photosynthetic forms below from the nonphotosynthetic forms above. Where a phylum contains both photosynthetic and nonphotosynthetic types, the name of the group appears with the more abundant types. The letters in conjunction with the algal groups refer to the variants of chlorophyll present. Note that, in virtually all cases, exact interrelations are not yet known and that the lines of interconnection must be regarded as provisional.



REVIEW QUESTIONS

- 1. Describe the structural characteristics of bacteria and blue-green algae. In what respects are these two phyla alike? Different?
- 2. What features identify an organism as an alga? Describe the chief characteristics of the various phyla of green-line, brown-line, and red-line algae. Review also the (a) pigments, (b) food-storage compounds, (c) cellwall compounds, characteristic of these organisms.
- 3. Give examples of (a) unicellular, (b) multicellular, (c) colonial algae. In which algal phyla do both unicellular and multicellular types occur?
- 4. In what specific environments may be found (a) Spirogyra, (b) Fucus, (c) red algae, (d) brown algae, (e) dinoflagellates?
- 5. What is the probable evolutionary significance of pairs of algae where one is photosynthetic and the other not? Give specific examples of such pairs, for three or four algal phyla.

- 6. Describe the basic structure of all fungi. What diagnostic features distinguish the different classes? What representative kinds of fungi are included in the different classes? What makes a yeast cell a fungus rather than a bacterium?
- 7. Review the life cycle of slime molds. What justifies the inclusion of these organisms in the Protista?
- 8. Describe the diagnostic group characteristics of protozoa. What features uniquely distinguish the various protozoan phyla? What are foraminifera? Radiolaria? Describe the structure of a ciliate protozoon.
- 9. What are the unifying features of the Protista? Why are its various groups no longer classified simply as "plants" and "animals"? Describe the probable ancestral type from which Protista are believed to have evolved.
- 10. Review the complete taxonomic classification of man. What defines a "phylum"? A "species"?

SUGGESTED COLLATERAL READINGS

- Chapman, V. F.: "Seaweeds and Their Uses," Methuen, 1950.
- Clayton, R. K., and M. Delbruck: Purple Bacteria, Sci. American, vol. 185, 1951.
- Henrici, A. T., and E. J. Ordal: "The Biology of the Bacteria," Heath, 1948.
- Milner, H. W.: Algae as Food, Sci. American, vol. 189, 1953.
- Russell, P. F.: The Eradication of Malaria, Sci. American, vol. 186, 1952.
- Weiss, F. J.: The Useful Algae, Sci. American, vol. 187, 1952.

CHAPTER 8

Metaphyta: advanced plants

Included in the Metaphyta are all the green, terrestrial, multicellular plants. As noted earlier, their evolutionary derivation from ancestral green algae is strongly suggested by the presence of chlorophylls a and b, by cell walls made of cellulose, and by the deposition of food stores in the form of starch. Metaphyta are distinguished from their protistan relatives by possessing usually complex multicellular sex organs and by the occurrence of more or less distinct embryonic stages during the development from egg to adult. As noted also, Metaphyta have lost the centrioles.

Two major independent lines of Metaphyta have

evolved, represented today by two phyla, the bryophytes, or moss plants, and the tracheophytes, or vascular plants. The latter are the far more important, abundant, and spectacular, and they will occupy most of our attention in this chapter.

BRYOPHYTES

Early moss plants, evolved from aquatic ancestors, had to solve the problem of surviving in a terrestrial environment. This meant, for example, that they had to develop protection against evaporation, means to resist the effects of gravity, and means to

reproduce without permanent bodies of water. Bryophytes actually have had only limited success in these respects. Even now they are small-bodied plants, their principal support against gravity being the solid ground, along which they grow. And moss plants live in more or less shady, perpetually moist places, where the danger of drying out is minimized and where rain water is often available as a medium for swimming reproductive cells.

Phylum BRYOPHYTA: moss plants (25,000 species)

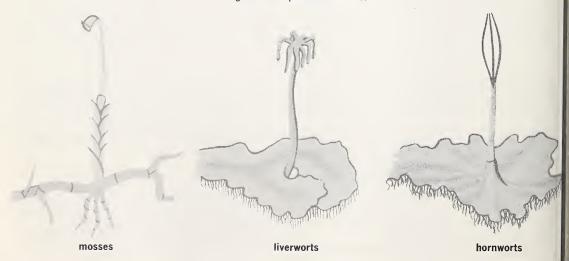
Class Musci: mosses
Sphagnum, Mnium
Class Hepaticae: liverworts
Marchantia, Sphaerocarpus
Class Anthocerotae: hornworts
Anthoceros

Mosses are now believed to be the most primitive members of the phylum. The body of a moss consists of fine threadlike strands of green cells, spread flat over the ground. Small extensions in places project into soil, and these serve for absorption of water and minerals. At certain seasons of the years, upright, more or less radially symmetrical outgrowths form at different points along the flat mesh of strands. These outgrowths bear tiny leaflike blades, and at the top of such a structure the sex organs develop (Fig. 8.1). We shall discuss the reproduction and the life cycle of mosses in Chap. 20.

In liverworts, the ground-hugging plant body resembles a notched leaf with midribs. Hornworts are flat and prostrate too, but the plant body is not notched and it does not have midribs. In both of these classes, reproductive organs often develop on stalked outgrowths as in mosses (Fig. 8.1).

Bryophytes as a whole have remarkable powers of regeneration, and many have developed a very specialized method of nonsexual reproduction. This involves gemmae, which are small cup-shaped growths on the surface of the plant body. If such a

FIG. 8.1. Bryophytes (diagrammatic). Representative individuals of the three classes are drawn. See also Chap. 20 for other illustrations of bryophytes. The upright outgrowths are reproductive structures.



gemma is dislodged from the parent and is deposited on suitable ground, it may develop into a whole new plant (Fig. 8.2).

TRACHEOPHYTES

The plants in this huge phylum are distinguished by the presence of specialized conducting, or vascular, tissues: channels which carry water, minerals, and food within the plant. Because such a "circulatory system" is present, vascular plants may attain considerable size; and because they also evolved efficient antigravity supports (for example, wood), they may grow away from the ground and become tall and upright. Another identifying feature of the group is the more or less clear-cut subdivision of the plant body into roots, stems, and leaves. Tracheophytes have also developed efficient evaporation-resisting devices (see below) and efficient means to reproduce away from bodies of water. As a result of these evolutionary innovations, tracheophytes have become the dominant plants of today. Four major subgroups are recognized, each of subphylum rank. Fossil data suggest that one of the subphyla, the psilopsids, may be ancestral and that the other three have evolved independently from early psilopsid stock.

Phylum TRACHEOPHYTA: vascular plants

Subphylum Psilopsida

Psilotum (2 species), Tmesipteris (1 species) Subphylum Lycopsida

Club mosses

Lycopodium (100 species), Selaginella (500 species)

Subphylum Sphenopsida

Horsetails

Equisetum (25 species)

Subphylum Pteropsida

Class Filicineae: ferns (10,000 species)

Class Gymnospermiae: conifers, cycads, gink-goes (600 species)

Class Angiospermiae: flowering plants

(200,000 species)

The first three subphyla above, spectacularly suc-



FIG. 8.2. The liverwort Marchantia, showing gemma cups. (Carolina Biological Supply Co.)

cessful in the past, today are little more than evolutionary relics. Of the psilopsids, only three species now remain and they still feature characteristics remarkably similar to those of their fossil ancestors. *Psilotum* grows with forked branches, very small scalelike leaves, and bulbous spore cases near the leaves (Fig. 8.3). The life cycle resembles that of a fern, and this is true also for lycopsids and sphenopsids (Chap. 20).

The lycopsids, or club mosses, are more widely represented today, and the ground pine *Lycopodium* in particular is still relatively common (Figs. 8.3 and 8.4). This lycopsid possesses forked stems covered with small, somewhat needle-shaped, spirally arranged leaves and terminal cones containing spore cases.

The living sphenopsids, or horsetails, all belong to the single genus called *Equisetum*. This particular group is characterized by small scalelike leaves, arranged in whorls at the nodes of hollow stems. Spore-bearing cones grow at the tips of the stems (Fig. 8.3).

The pteropsids today include the most abundant and most important of the terrestrial plants. An ancestral pteropsid group probably arose from early psilopsids and subsequently branched into two main lines, one leading to the modern ferns, the

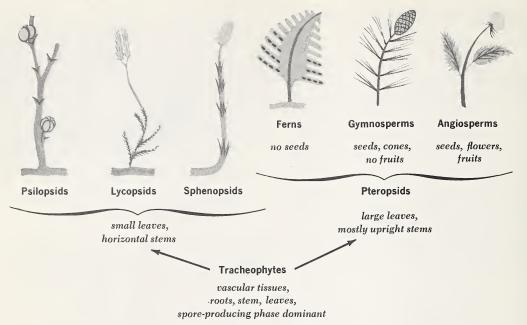


FIG. 8.3. The subphyla of tracheophytes and the classes of pteropsids. Some of the diagnostic features of each group are shown.

other to the seed plants. The latter include the modern gymnosperms and angiosperms (see also Chap. 24). All three pteropsid classes evolved large leaves, very distinct from the foliation patterns in the other tracheophyte subphyla. Undoubtedly, this contributed greatly to the past and present success of the pteropsids. In Chap. 20 we shall also see how the seeds of gymnosperms and angiosperms enhanced the adaptation of these two classes to terrestrial conditions (Fig. 8.3).

A very abundant group in past ages, ferns today inhabit few areas other than tropical rain forests, where many still reach the dimensions of trees. The far smaller ferns of temperate regions feature roots which extend from horizontal stems growing on, or just under, the soil surface.

The gymnosperms were the first seed plants. The

earliest representatives of the class were rather fernlike in appearance, and some of these fossil gymnosperms are actually called, rather misleadingly, "seed ferns." The living cycads still resemble ferns superficially. Ginkgoes are another example of a once abundant group, now reduced to a single species. The most common gymnosperms today are the *conifers*, of which the pines, firs, and spruces are familiar examples.

The angiosperms are the most varied and most abundant group of all plants. They differ from other pteropsids principally in the possession of flowers and fruits and in certain other features of reproduction to be discussed in Chap. 20. The exact ancestry of angiosperms is unknown, but it is generally believed that they arose from early gymnospermlike seed plants. They are therefore the most

recently evolved of all plants, but they have become so successful that they have replaced all other terrestrial plants to a very large extent.

Flowering plants today inhabit virtually all environments except the open ocean. They include aquatic types, parasitic types, saprophytic types, and partly carnivorous types. They enrich the world with color and scent, but they also exude poison and stench. Some survive only a single growing season; others live for centuries. Some complete an entire generation, from seed to seed, within a few days; others require decades. And we may note here that terrestrial animals owe their continued existence largely to angiosperms, for these plants are the essential food producers for all life on land.

The remainder of this chapter is devoted to a more detailed discussion of the organization and structure of tracheophytes. Many of the particulars apply to the vascular plants generally, but unless otherwise specified, flowering plants are the group we shall be particularly concerned with.

PATTERNS OF LIFE

Since tracheophytes are photosynthetic, they need not hunt for food like animals. Active locomotion therefore does not become necessary. This absence of a requirement for propulsion affects the entire structural and functional organization of a tracheophyte. Thus muscles, and nervous systems which control muscles, are not present. But the permanently stationary plant is adapted to a nutrientsupplying two-phase environment, so that roots obtain some raw materials from below ground and leaves obtain others from aboveground. Further, the plant is radially symmetrical around its vertical axis, a design which provides both balanced anchorage in soil and broad exposure to sun and air. The plant stem generally tapers upward, which results in greater support against gravity nearer the bottom, where the top weight is greater.

However, appropriate physical design is not

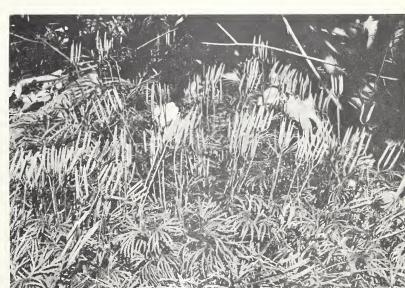


FIG. 8.4. Living lycopsids. The ground pine Lycopodium is shown. (Brooklyn Botanic Garden photo.)

enough for survival on land. A terrestrial organism which cannot move also must cope with potentially lethal changes in local weather. Water here poses the key problem. Water tends to evaporate, particularly so during the heat of summer, and in winter water tends to freeze, which would kill protoplasm.

As safeguards against evaporation, plant leaves and other soft tissues exposed to air secrete waxy coats over their outer surfaces. These transparent cuticles let sunlight through readily, and they prevent the escape of internal water. But in so doing they also bar the entry of gases from the atmosphere. Yet carbon dioxide and oxygen must be absorbed. The dilemma is resolved by the presence of microscopic surface openings, called stomata (see below). Distributed in considerable numbers over green tissues, these openings permit absorption of raw materials and permit also a good deal of evaporation. But the greater part of the tissue is protected by wax, and a large surface is still available for illumination by sunlight.

In warm dry climates, the wax cuticles over exposed surfaces may attain considerable thickness.

FIG. 8.5. Under desert and near-desert conditions, the stomata of a plant may be located at the bottom of microscopic pits in the leaf surface, as illustrated in this photo. Many desert plants in addition possess very thick waxy cuticles (not shown here) secreted by the cells of the leaf epidermis. (Courtesy of J. M. Bell, Polytechnic Institute of Brooklyn.)



Also, stomata are often reduced in number. They are found on the undersides of leaves, where shade and somewhat lower temperatures reduce evaporation and where dust is not so likely to clog them. Or they may be situated deep in microscopic leaf-surface pits, which provide shade except when the sun shines straight into them (Fig. 8.5).

Under near-desert conditions, the rate of evaporation may nevertheless be too great. Water vaporization can be held down, however, by reducing the area of exposed parts. In persistently dry regions, plants may possess fewer leaves (palms) or succulent, bulky, water-storing leaves (as in many ornamental house plants), and stems may grow underground or may be much decreased in size. Or, as in cacti, leaves may be represented merely by thorny spines and massive stems take over the function of food manufacture (Fig. 8.6).

Through adaptations such as these, plants are able to survive even in the hottest, driest regions, provided that at least *some* water is available at *some* time.

A summer day may be excessively hot and dry, and the tracheophyte may droop and begin to wilt. But if the following day brings moisture, conditions within the plant are soon restored to normal. By contrast, winter frost for even an hour is likely to kill. For below the freezing point, water which is not firmly bound in colloidal gels is transformed into ice crystals. Such crystals tear and disrupt the protoplasmic framework. Therein lies the lethal effect of cold.

In response to seasonally recurring low temperatures, major adaptations have developed in tracheophytes which profoundly affect their whole way of life. On the basis of these adaptations, we may distinguish three groups of vascular plants: perennials, biennials, and annuals. The first group includes woody plants and some of the herbaceous forms (soft-stemmed herbs). The second and third groups comprise all other herbaceous plants.

In *perennials*, major portions of the plant body persist through successive winters. Icing up is reduced or prevented altogether. For at the approach



FIG. 8.6. A variety of cacti, plants adapted to desert conditions. Leaves are reduced to spines, and the green stems have taken over the function of food manufacture and water storage. (General Biological Supply House, Inc.)

of winter, large quantities of colloidal gums and resins are manufactured. This increase in the amount of colloid particles converts much of plant protoplasm into a gel state. As a result, little water remains free inside cells and freezing is successfully forestalled.

In coniferous evergreens like pines, such winterproofing, or winter hardening, is particularly effective. Even leaves can be retained, and vital processes carry on as in summer, though at a much slower pace.

The other woody perennials, called *deciduous* plants (e.g., flowering trees), cannot protect their foliage against the cold. Leaves are shed in the fall, but the rest of the organism lives on. Tiny leaf buds, developed during the preceding summer, sprout forth in the spring as new foliage. In the absence of mature leaves during the cold season, food cannot be produced. However, these woody types accumulate food reserves at other seasons and store them in root and stem.

In herbaceous perennials (e.g., asparagus, dandelion), both leaves and stem die off in the fall and only the roots survive. Where the root branches join together, just under the soil surface, there is usually a small remnant of stem which survives the winter also, along with the roots. Reserve food in the roots lasts through the winter and suffices in spring for the development of a little green tissue. Thereafter, new stem and leaf systems sprout rapidly. Since they persist only through a relatively short growing season, the aerial portions of these plants never become very extensive. Bulky supporting wood is neither required nor formed, and roots stay relatively small.

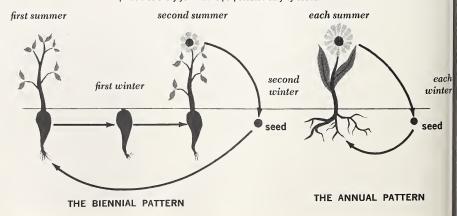
The above patterns (Fig. 8.7) give evidence of an adaptive trend among perennials: it is more economical to retrench when life becomes difficult than to maintain elaborate aerial superstructures against heavy odds. This trend does not halt here, however. Winter retrenchment goes even further in biennial and annual herbaceous plants.

In biennials (e.g., carrot), leaves and stem die off in a first winter, after procuring extensive food reserves which are stored in bulky roots. The roots survive that winter, and from them develops a new plant in the following spring. This second-year plant flowers, reproduces, and forms seed. Then the entire plant dies, roots included. Only the seeds survive, and these subsequently initiate a new 2-year cycle (Fig. 8.8).



FIG. 8.7. The perennial patterns among plants. In one pattern, as in conifers (left), the whole plant survives the winter. In another pattern, as in deciduous plants (middle), foliage is shed in the cold season but the rest of the plant survives. And in a third pattern, as in herbaceous perennials (right), only the roots and a small remnant of stem survive the winter.

FIG. 8.8. The biennial and annual patterns among plants. In a biennial, only the roots survive a first winter and only seeds survive a second winter. In an annual, the whole plant dies every year and is perpetuated only by seeds.



The annual plant (e.g., wheat, corn) flowers and produces seed every year. The whole plant dies in the fall, and its seeds give rise to a new generation in the following spring (Fig. 8.8).

The immobile land plant, we note, finds several workable solutions to the problem of cold. It may winterproof its whole body or a larger or a smaller part of its body, or it may rely entirely, and most economically, on a handful of hardy cells: seeds, which often contain as little as 5 per cent water and are even hardier than the hardiest Christmas tree.

Thus tracheophytes have made the most of their difficult environment. Actually only two climatic extremes can stop the flourishing of the terrestrial plant: glacial temperatures, as at very high altitudes and latitudes, and permanent lack of water, as in some deserts. And where the food-producing green plant cannot live, very little else can live either.

INTERNAL STRUCTURE

We begin this inquiry into tracheophyte structure with a discussion of stems. For more than the leaf or the root, the stem is the distinctive hallmark of the tracheophyte. A violet, a bamboo, and an apple tree are quite obviously different. And of all their differences, those of their stems are the most pronounced.

Stems: herbaceous types

Imagine that the seed of a herbaceous plant—a corn plant, or a buttercup, for example—has germinated just recently and that a young *seedling* has become anchored in soil. A *shoot* already projects above ground. Transformation of this seedling into a mature plant involves *growth*, brought about largely by the repeated division of cells in so-called meristem tissues. These are present in particular regions and are composed of permanently embryonic cells. The new cells formed by division specialize, form adult tissues, and normally do not divide thereafter. Only the meristem cells retain a high division potential.

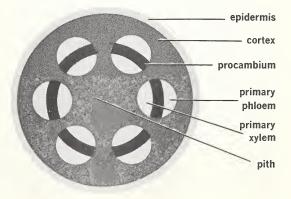
One meristem region, the apical shoot meristem,

is situated at the shoot tip. When an embryonic tip cell divides, one of the daughter cells remains in the space originally occupied by the mother cell; the other daughter cell is pushed ahead. Thus the tip advances, and the shoot grows in length. The youngest part of the plant consequently is at the upper stem terminal, the oldest part, at the stem base.

As the shoot tip advances, the cells behind it soon specialize and form concentric layers of tissues. From the outside to the center (Fig. 8.9), these layers are as follows:

- 1. Surface cells flatten out and secrete an external waxy coat. A transparent skin, the epidermis, arises in this manner. Made of a single layer of cells, this tissue becomes continuous with the epidermis of lower stem levels, laid down at earlier stages. Some of the epidermis cells take part in the formation of stomata, microscopic openings for gas exchange, as on leaves.
- 2. Cells just underneath the newly formed skin specialize as a space-filling "packing" tissue, the parenchyma. The layers of this tissue develop chlorophyll and the metabolic machinery for food production. All the shoot below the specialization zone appears green therefore, and this portion of

FIG. 8.9. The basic pattern of cross-sectional specialization of the tissues in a young shoot of a herbaceous plant. Note the ring of vascular bundles, each composed of three tissues.



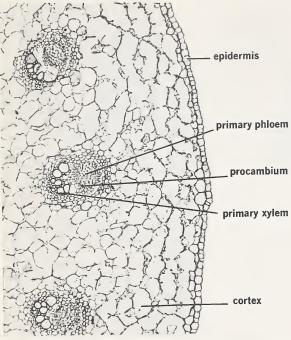


FIG. 8.10. Cross section through the stem of a buttercup. Note the spacing of the vascular bundles and the tissues within each bundle. (General Biological Supply House, Inc.)

the shoot aids materially in the nutrition of the young seedling.

3. In a region roughly midway between the epidermis and the center of the stem and embedded in parenchyma, bundles of tissue appear. These bundles are arranged roughly like fence posts in a circle, and each bundle is surrounded by parenchyma. The parenchyma tissue between the ring of bundles and the epidermis is called the stem cortex, and the tissue within the ring of bundles, the stem pith. A bundle itself is known as a vascular bundle (Fig. 8.10).

Each such bundle consists of three kinds of tissues (Fig. 8.10). One of these is a single layer of embry-

onic cells, which marks off an outer and an inner part in the vascular bundle. This layer of embryonic cells is called **procambium**. In herbaceous plants it is of little further significance. In buttercup stems, for example, it simply persists as a nonfunctional layer, and in corn stems it eventually disappears altogether as a distinct tissue.

The tissue toward the inside of the procambium consists of so-called xylem cells. The protoplasm of these cells soon disintegrates, and only the hollow cell walls remain. An original vertical column of xylem cells so gives rise to a channel of nonliving cellulose, a so-called xylem vessel. Such vessels come to extend through the entire length of the stem and indeed also through the roots and the leaves. Xylem vessels represent one of the two conducting, or "vascular," tissues of the plant. Water and minerals absorbed by the roots are transported upward through the xylem.

The second type of conducting tissue develops from the cells in the outer part of a vascular bundle. This is known as phloem tissue. In the development of this tissue, cells in vertical columns disintegrate partially; that is, the nuclei break down. Moreover, the top and bottom cellulose walls of these cells

FIG. 8.11. Diagrammatic representation of a unit of phloem tissue. Note the nucleated companion cell, the sieve plates, and the nonnucleated sieve tube. In the living state, cytoplasm fills the sieve tube completely; the contracted condition of the cytoplasm shown here is typical only of killed and fixed microscopic preparations.



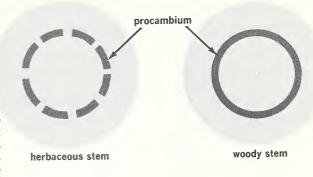
FIG. 8.12. Diagram of sections through herbaceous and woody stems. In a herbaceous stem, the procambium occurs in circularly arranged strips. In a woody stem, the procambium forms a complete tube.

develop fine perforations. The perforated cross-walls are then known as *sieve plates*. A vertical column of such sieve-plate-equipped, partially disintegrated cells is termed a **sieve tube**. Intimately associated with each sieve tube is a column of normal cells, called **companion cells**. They probably control the functioning of the adjacent, nonnucleated sieve-tube protoplasm (Fig. 8.11). The function of phloem is downward and upward conduction of organic nutrients.

We note that both vascular tissues of the stem, namely, xylem and phloem, develop through the partial disintegration of vertical columns of cells and the more or less complete retention of the cellulose walls, which form tubes. Hence the designation "tracheophyte," or "tube-possessing plant."

With the formation of bundles of xylem and phloem, the development of the herbaceous stem is essentially complete. Note that such stems grow principally in length, all new additions of tissue being made by the apical shoot meristem. Because the vascular tissues here originate from the apical meristem, they are called *primary xylem* and *primary phloem*. Growth in thickness in herbaceous stems is mainly a result of growth in cell *size*, aided by absorption and retention of water. Since stem cells nearest the ground are the oldest and have grown in size the longest, they are larger than cells nearer the stem tip. Hence herbaceous stems may develop an upward taper.

In so-called semiherbaceous plants, of which the sunflower is a good example, development of the oldest stem parts, i.e., those nearest the ground, proceeds further than indicated above. In such stem regions a woody condition develops. This is brought about by continued growth of the procambium.



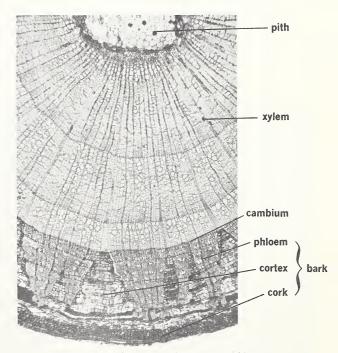


FIG. 8.13. Photo of a cross section through a fairly young woody stem, showing internal tissues. (General Biological Supply House, Inc.)

More specifically, the procambium layers of neighboring vascular bundles grow toward one another until they meet and fuse. A complete ring (or, in three-dimensional view, a tube) of procambium is formed in this way (Fig. 8.12). This eventually leads to a woody condition just as it does in wholly woody stems, and we shall describe the process in the following section.

Stems: woody types

The early development of a woody stem is substantially similar to that of a herbaceous one; i.e., stems of young woody plants are green and soft too. The essential difference lies in the activity of the procambium. First, this embryonic tissue forms as a complete tube, as just noted above. Second, it remains functional; that is, its cells divide frequently, and new cells so produced are pushed either to the outside or to the inside of it. Because of this persisting activity, the procambium is now called cambium.

The cells which proliferate outward from the cambium specialize as phloem tissue, and the cells which cambium produces toward the inside of the stem become xylem vessels. Because these vascular tissues here arise from cambium, not apical meristem, they are referred to as secondary phloem and secondary xylem. Such secondary growth contributes to a great enlargement of the thickness of the stem. Indeed, the secondary xylem, growing layer by layer from the whole ring of cambium inward, compresses and largely displaces the pith parenchyma it encounters. Eventually this inward growth can no longer continue, and any additional xylem formed by the cambium can then produce only outward expansion. This increases the thickness of the stem. Secondary xylem formed in extensive masses, as in such woody stems, constitutes the main component of wood (Figs. 8.13 and 8.14).

Secondary phloem tissue, growing outward layer by layer from the cambium displaces earlier tissues already there. Eventually, the outer epidermis and

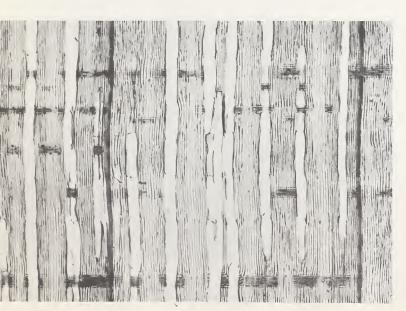


FIG. 8.14. Longitudinal section through wood, showing xylem channels. The two dark vertical lines mark out an annual ring. (General Biological Supply House, Inc.)

cortex tissues rupture from the growth pressure against them. Fissures so form, and underlying tissues come to protrude through them. Under the drying influence of air, the protruding cells of the cortex then develop into so-called **cork cambium**. This layer produces *cork cells*, which secrete a very efficient waterproofing material known as *suberin*. Suberin-coated cells now form the surface of the stem. All tissues between this surface of cork cells and the cambium together represent **bark**. As stem girth enlarges, bark ruptures repeatedly, and as new bark-forming tissues grow outward from cambium and cork cambium, older bark on the outside flakes off (Fig. 8.13).

These processes slowly transform the green shoot of the young woody plant into a taller, thicker, tapering woody stem. Note that formation of wood and bark proceeds from the ground upward.

Parallel with these events, branching growth takes place. The base of each leaf on a stem is the area of a node. The length of stem between two successive nodes is called an internode (Fig. 8.15). Branching growth occurs only at nodes. Lateral buds may arise here which grow out at an angle. Branch stems develop in length and in thickness like the main stem. Wood and bark form progressively from the base forward. At the base of the branch, the vascular tissues, phloem and xylem, become continuous with those of the main stem. Branches which angle off nearest to the ground are older and have grown longer than branches farther up. Hence the familiar upward taper of the branch system of a tree.

The above pattern of growth is repeated again when secondary branches develop from primary ones. At the upper nodes of a young primary branch, leaves may first appear. Secondary branch stems may then form there later. From these, new leaves and tertiary branch stems develop in turn. We note that a small outer branch with its leaves is, in effect, a replica of the original shoot from which the adult tree has grown.

In cut sections of older stems, such as mature tree trunks, the naked eye identifies only bark and

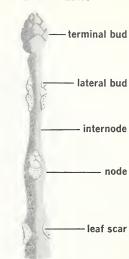


FIG. 8.15. Diagram of a dormant stem with buds.

wood. The microscope, however, reveals the single layer of cambial cells, at the line of juncture between bark and wood, and reveals also that the inner part of "bark" is actually phloem.

Only young phloem and xylem are functional. Older phloem tissue ruptures, becomes part of bark, and flakes off. Older xylem, near the pith, becomes heartwood. Its vessels may gradually block up with resins and gums, and water conduction through them is then no longer possible. The core of a tree may therefore be hollowed out without interfering with water conduction. But the outer, younger wood of a tree, called the sapwood, must remain intact if a tree is to remain alive. A tree dies when it is "ringed," that is, when a cut around the circumference interrupts the vertical continuity of phloem, or of phloem and sapwood together.

Annual rings are fairly conspicuous in an older stem (Figs. 8.14 and 8.16). Xylem vessels formed during spring generally have a larger diameter than those formed in summer. In spring, melting snow provides the tree with much water. Wider conduct-



FIG. 8.16. Portion of a 12-year-old tree trunk, showing annual rings. (U.S. Forest Service.)

ing vessels are then developed, which may accommodate the greater flow. The alternation of narrow summer xylem and wider spring xylem is recognizable with the naked eye as concentric dark and light banding—annual rings. The number of rings indicates the age of a tree. Moreover, from the comparative widths of spring and summer rings it is also possible to estimate the amount of rainfall, hence general climatic conditions, during past seasons, as far back in time as the tree has lived.

Roots

On the whole, the principal pattern of root growth is remarkably similar to that of stem growth. However, roots carry out a number of different functions, in a different environment. Hence correlated differences in organization may be expected.

In the young seedling, cells of an apical root meristem divide, just as in the stem. One difference between root and stem is that the apical root meristem pushes some of the newly formed cells ahead of it. These outermost cells of the root tip form a rootcap (Fig. 8.17). This is an important adaptive device, for as the root tip advances, hard soil grains would soon macerate unprotected meristem tissue. In the presence of a rootcap, however, cap cells wear off instead and the growing tip is shielded effectively. New cap cells are formed continually by the meristem.

As in the stem, surface cells behind the meristem

become epidermis. Root epidermis, which absorbs soil water and dissolved minerals, develops neither stomata nor waxy surface coating. Instead, root hairs appear. These are delicate fingerlike extensions of certain epidermis cells, providing a tremendously increased surface area for absorption (Fig. 8.17). Absorbed water soon passes into the cells underneath the epidermis. As these cells swell with fluid they elongate greatly; this generates a push from behind, an important factor in forcing the root tip through soil.

Root hairs persist only for a short while. When an epidermal cell ages, its absorptive hair is lost. A distinct root-hair zone may therefore be found some distance behind the meristem tip. Ahead of this zone, root hairs have not yet developed; behind it, they have already disappeared. Continued existence of the plant depends on daily extension of its root system, for hair zones must be available at all times.

The root epidermis is underlain by layers of cortical parenchyma. The innermost cortex layer is specialized as an endodermis (Fig. 8.18). Like the cork cells of bark, endodermal cells manufacture suberin, though not so extensively as cork cells. This substance impregnates portions of the endodermal cell walls. Endodermis thus serves as a waterproofed layer which encloses the core tissues of the root. Numerous passage cells within the endodermal layer remain soft and unsuberized, permitting the unhindered transmission of water from epidermis and cortex to the interior root xylem.

In any root, regardless of which stem type is associated with it, the vascular tissues are aggregated compactly within the cylinder of endodermis. Pith is not present, and xylem vessels occupy the central space. In a cross-section view, the arrangement of these vessels somewhat resembles the spokes of a wheel, the outer ends of the spokes abutting against the endodermal passage cells (Fig. 8.18). Phloem fills the spaces between the spokes. In woody and semiherbaceous plants, cambium is present between phloem and xylem. Root cambium here may in time produce so much vascular tissue that epi-



FIG. 8.17. A root showing the root-hair zone. At lower tip, note the thickening formed by the rootcap. (General Biological Supply House, Inc.)

dermis, cortex, and endodermis are ruptured. Bark is then formed. In an older woody or semiherbaceous plant, therefore, root merges imperceptibly into stem near the soil-air boundary.

If the plant is wholly herbaceous, root cambium may be present but it may be nonfunctional, or it may not be present at all, as in corresponding stem types. In either case, increase in thickness does not occur and roots remain nonwoody. The transition to stem is then more abrupt. Near the soil-air boundary, the conducting tubes of the root become segregated in distinct vascular bundles, and these are continuous with the phloem-xylem bundles of the stem.

Unlike stems, roots do not possess nodes and branching may occur at any point. A number of patterns may be distinguished. For example, many branch roots may lead off from the stem base in all

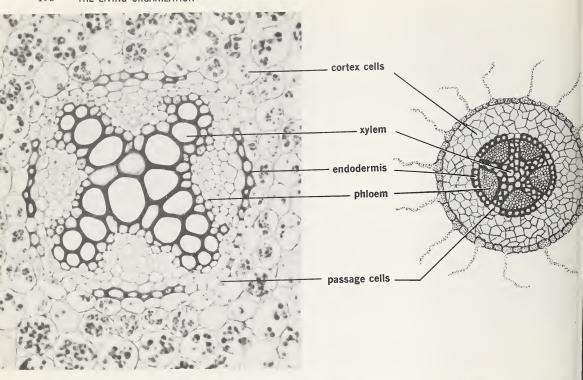


FIG. 8.18. Diagram: cross section through a root at the level of the root-hair zone. Photo: enlarged sectional view of the central tissues of a root. The dark granules in cortex cells are starch-storing bodies. (Photo, General Biological Supply House, Inc.)

directions, as in the fibrous roots of grasses. Or a single strong taproot may penetrate vertically into the ground and smaller secondary roots may radiate out along its course (e.g., dandelions, carrots). Such roots usually possess extensive cortical parenchyma, an adaptation for food storage. (Slice a carrot across and observe. Note, incidentally, that a potato is a *stem;* that an onion is a concentric system of *leaves*, arising from a flat disklike stem; that roots, stems, and leaves may all be adapted for food storage; and that what is pulled out of the ground evidently is not automatically a root.)

Not all roots connect with the stem base; some sprout from anywhere on the stem. Such adventitious roots are found, for example, on the horizontal underground stems of a number of seed plants. The banyan tree possesses adventitious roots, which here are called **prop roots**: root branches arch away into the ground from high up on the upright aerial stem (Fig. 8.19). In older corn plants, prop roots are usually encountered too, leading off from the lowest nodes of the stem.

Orchids have aerial roots, nowhere in contact with soil. These roots are adapted to absorb rain



FIG. 8.19. An illustration of prop roots. (Brooklyn Botanic Garden photo.)

water directly as it falls. A parasitic aerial root is in evidence in the mistletoe. Equipped with suckers, these roots hold on to the host tree, and water is siphoned off from the host xylem.

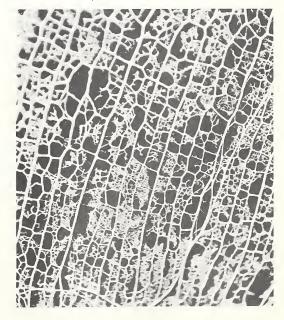
These few examples show that roots have adaptive versatility of their own. Being one with the rest of the organism, an adapted root is a prerequisite for an adapted plant. But roots, as well as stems, are largely subservient to the leaves. These are unquestionably the most essential parts of a plant. A single isolated leaf may be put into a glass of water rich in minerals, and when exposed to sunlight, this leaf may survive. But an isolated root or a stem without green tissue soon dies under similar conditions. Root and stem make the functioning of the leaf possible, and thereby they ensure their own persistence.

Leaves

Everyone is familiar with needle-shaped, net-veined, and parallel-veined leaf types. In all, the leaf blades are usually connected to stem nodes through petioles, woody or green stalks structured essentially like thin stems.

Regardless of whether or not the plant is woody or herbaceous, small aggregations of xylem, phloem, and fiber tissue branch off from the stem and pass uninterruptedly into the leaf as vascular bundles. These are the veins of the leaf. Either they ramify in intricate patterns or they continue in parallel. They provide physical support, and they constitute the upper terminus of supply lines which reach without break from the farthest root tip to the farthest leaf tip (Fig. 8.20).

FIG. 8.20. The pattern of the veins in a leaf. (Brooklyn Botanic Garden photo.)



Cambium does not branch away into the leaves. Neither is there a distinct meristem tissue. Indeed, leaf growth differs fundamentally from either root or stem growth. In a leaf bud, the *whole* leaf is laid down in miniature. Subsequent growth is principally a matter of cell enlargement, boosted now and then by cell division. This takes place in all parts of the leaf simultaneously. If a rectangular grid were drawn on an immature blade, the mesh width of the grid would increase as the leaf grows. But straight lines would remain more or less straight, and the regularity of the grid would be preserved.

An epidermis covers the outside of the leaf (Fig. 8.21). This layer is continuous with the stem epidermis, if present. The epidermal cells of the leaf are transparent, and they are coated with a waxy cuticle of varying thickness. With the exception of cells which form stomata, epidermal cells do not contain chloroplasts.

A stoma (plural: *stomata*) is a pore enclosed by a pair of crescent-shaped, chloroplast-containing guard cells (Fig. 8.22). The walls of these cells are thickest, hence stiffest, on the side which lines the pore. By virtue of this, a stoma can open or close

when the water volume increases or decreases within the guard cells. Since these cells are equipped with chloroplasts, they may produce carbohydrates. This increases the concentration of protoplasmic particles. As a result, water from surrounding epidermal cells is drawn osmotically into the guard cells. As these swell, their thin outer side walls curve out under tension. This pulls the inner thicker side walls apart, and the stoma opens. Conversely, when carbohydrates are being used up, the water volume of guard cells decreases. The elastic cell walls then revert to their original position, and so the stoma closes.

This device regulates the rate of gas exchange (oxygen, carbon dioxide, and water vapor) between the atmosphere and the leaf interior. Stomata open wide, moderately, or not at all, in accordance with specific conditions of humidity, temperature, and lighting. For example, on a very dry, hot summer day, the leaf pores are almost fully closed. The rate of photosynthesis in the leaf is then reduced, inasmuch as not enough carbon dioxide can enter. But the evaporation of internal water, a problem of more immediate concern, is held down at the same time. As noted earlier, stomata may be present on

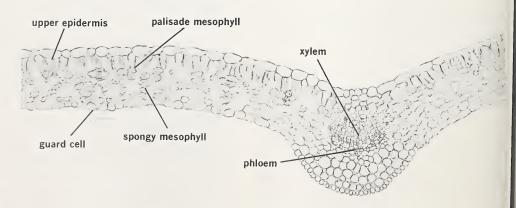


FIG. 8.21. Photomicrograph of a section through a leaf. The large vein shown represents the midrib of the leaf. (General Biological Supply House, Inc.)

either or both sides of a leaf, their number per unit of surface area may vary, and they may be placed flush with the leaf surface or may be sunk into pits.

Wrapped in epidermis, mesophyll tissue fills the interior of the leaf (Fig. 8.21). This is the chief food-producing tissue of the plant: all mesophyll cells contain chlorophyll. Just underneath the upper epidermis in horizontally placed leaves, and underneath the whole epidermis in most upright and needle-shaped leaves, mesophyll cells are arranged in compact layers, or palisades. Elsewhere, mesophyll is spongy; that is, it is organized into loose cellular strands and layers. The whole is honeycombed extensively with air spaces. These connect with one another and lead to the exterior of the leaf through open passages in the palisade tissue and the stomata. This structural arrangement brings the greater part of every mesophyll cell into direct contact with fresh external air. Leaf veins ramify abundantly through the mesophyll, and no green cell is very far removed from these channels.

We have reached the heart of the leaf, indeed the heart of the whole plant: the individual mesophyll cell. Considered by itself, such a cell is rather like a simple photosynthesizing algal cell floating in the sea. In the evolutionary transfer of such a cell onto land, the price of survival evidently has been a complicated plant body made up of a billion other cells, carrying out a trillion other reactions, to house it, support, it protect it, supply it, perpetuate it. That price evidently has not been too high. It has been paid gradually through slow evolution,

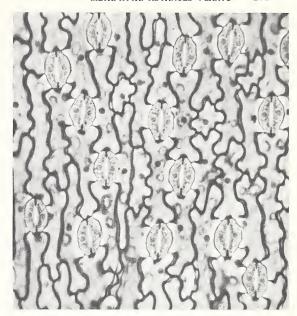


FIG. 8.22. Photomicrograph of the epidermis of a lily leaf, surface view. The dark lines outline epidermis cells. Note the pairs of guard cells enclosing the stomata. (Ward's Natural Science Establishment, Inc.)

at compound interest in adaptation. The result has been the eminently successful spreading of the terrestrial, photosynthetic way of life.

REVIEW QUESTIONS

- 1. Describe the basic structure of all bryophytes. What are gemmae?
- **2.** Describe the group characteristics of (*a*) the phylum Tracheophyta, (*b*) the tracheophyte subphyla, (*c*) the pteropsid classes.
- 3. Review the general structure of psilopsids, lycopsids, and sphenopsids. How are these groups related historically, and how abundant are they today?
 - 4. Review the adaptations of plants to land life. How

- do plants conserve water? How do they protect against winter cold?
- 5. What different groups of plants are perennial, biennial, and annual, and what life-cycle patterns define these groups?
- 6. What is the organization of semiherbaceous and herbaceous stems, and how do these differ from woody stems? How do vascular bundles develop?
 - 7. Show how a woody stem grows in length and in

thickness. Make sure that you understand the threedimensional structure of such a stem. What is the organization of xylem and phloem? How do these tissues develop, and what are their functions? In terms of tissues, what are wood and bark?

- 8. What is the cross-sectional structure of a mature woody tree trunk? Where in such a trunk are xylem and phloem? What are annual rings, and how do they develop?
- 9. Review the longitudinal and cross-sectional organization of roots. What tissues present in roots are not pres-

ent in stems? What are the functions of these additional root tissues? Conversely, what structures present in stems are not present in roots? What are the adaptive reasons for this? What are some of the branch patterns of roots?

10. Describe the external and internal organization of a leaf. How does leaf development differ from root or stem development? In what tissues does photosynthesis occur? What is the structure and distribution of stomata, and how do they function? Would you expect stomata to be open or closed at night?

SUGGESTED COLLATERAL READINGS

Anderson, E. A.: "Plants, Life, and Man," Little, Brown, 1952.

Mangelsdorf, P. C.: The Mystery of Corn, Sci. American, vol. 183, 1950.

----: Wheat, Sci. American, vol. 189, 1953.

Platt, R.: "Our Flowering World," Dodd, Mead, 1947.

Salaman, R. N.: The Social Influence of the Potato, Sci. American, vol. 187, 1952.

Schery, R. W.: "Plants for Man," Prentice-Hall, 1952.
Ward, H.: A Tour of a Tree, in I. W. Knobloch, "Readings in Biological Science," Appleton-Century-Crofts, 1948.

CHAPTER 9

Metazoa: advanced animals

That they arose from ancestral Protista is hardly in doubt, but it is impossible at present to be sure exactly which protistan group was directly ancestral. Early traditional views held that Protozoa gave rise to the Metazoa, but there is little evidence to indicate whether or not this is actually correct. Metazoa may equally well have originated from primitive flagellates directly. Indeed, there are some indications that different metazoan groups may have have arisen independently from various different protistan stocks. All we can be reasonably sure of at present is that Metazoa evolved when some

unicellular ancestral protistan group became multicellular and in the process retained powers of locomotion but lost any photosynthetic capacity it or they may have possessed.

Metazoa are all multicellular and clearly "animal" in character. They are distinguished from their protistan relatives in that their bodies are composed of distinct tissues and usually also of organs and organ systems. Moreover, they feature complex, multicellular sex organs, and their development passes through distinct embryonic and typically also larval phases.

Metazoa are classified into some 20 to 30 phyla.

In some cases universal agreement on phylum designations is lacking, hence the inexactness of the number of phyla.

ANIMAL CHARACTERISTICS

Nutrition and movement

Being nonphotosynthetic, all animals ultimately depend for food on photosynthesizers. Hence, both in space and in time, animal life waxes and wanes in step with plant life. From the standpoint of food sources, two broad categories of animals may be distinguished, the symbiotic and the free-living types.

Some of the animal symbionts live in mutualistic or commensalistic associations with individuals of other species (Chap. 4). But most are parasites, on or within specific hosts.

Free-living animals variously subsist on any protoplasmic matter available in the environment: living plants and animals, dead plants and animals, and many different kinds of protoplasmic derivatives, including in some cases decaying matter. Most of these free-living animals, and also most nonparasitic symbionts, are bulk feeders; they acquire nutrients in the form of bulk protoplasm. In other words, they have mouths and they eat (or ingest). Associated with this form of food intake is the process of digestion and the process of feces elimination, or egestion. Ingestion, digestion, and egestion together constitute the process of alimentation.

Animals are usually quite specialized in their eating habits. Thus herbivores are specialized to eat plant food. Carnivores subsist on other animals. And omnivores eat both animal and plant foods, living or dead.

Directly or indirectly, the whole organization of an animal is oriented by the requirement of alimentation. One immediate consequence is the necessity of locomotion. For whereas a plant finds raw materials practically all around it, bulk protoplasm is in strictly limited supply and its location generally does not coincide with the location of the hungry animal. Therefore either an animal must move toward food itself, or it may remain stationary and feed on moving animals which happen to pass by. We may note that numerous animal groups are specialized as permanently or temporarily sessile organisms (e.g., sponges, corals). All of them are aquatic, and many of them use their locomotor structures to create currents, which sweep small food organisms toward them.

Locomotion serves not only in food catching, but also secondarily in numerous other animal activities. For example, locomotion plays a fundamental role in mate selection and reproduction, functions which the mobile animal accomplishes far more readily than the sessile plant. Locomotion also is an important factor in protecting animals against environmental dangers, climatic change in particular. For example, as noted in Chap. 4, many animals carry out seasonal north-south migrations. Others remain at given latitudes permanently, yet through locomotion they are able to search out protective forests, caves, or self-constructed shelters like burrows, hives, nests, and houses.

Animal structure

The requirement of locomotion profoundly influences the external *form* of an animal. Most moving animals have an elongated, bilaterally symmetrical shape, which is particularly suited for locomotion. For propulsion of any kind necessarily implies that one portion of the organism "goes first" and that another goes last. Mechanical balance will be greatest if the left and right sides are equivalent, that is, if they are mirror images. And resistance by the propulsion medium will be least if the body is elongated in the direction of motion.

Moreover, the forward end enters new environments first. Sense organs for scouting and the chief nerve centers are therefore placed most advantageously at the front, and mouths should be located close to the sense organs. Thus the leading part of the animal becomes head. Analogously, elimination products of all kinds are best released at the hind end, where they do not impede forward progression.

A general build of this sort is actually standard and nearly universal among moving animals.

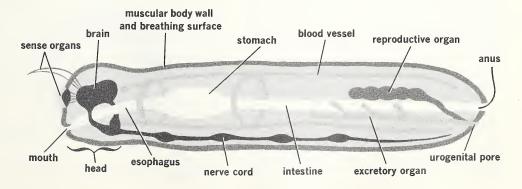
By contrast, sessile animals, and also many of the very slow movers, face their environment more or less equally from all sides, like plants, and their architecture reflects this. They are, or tend to be, radially symmetrical, and a distinct head is usually not present (e.g., corals, starfish). In many sessile forms also, the intestine is looped into a U, which brings the mouth and the anus close together and both openings away from the region where the animal is attached to the ground (e.g., tunicates, Fig. 9.34).

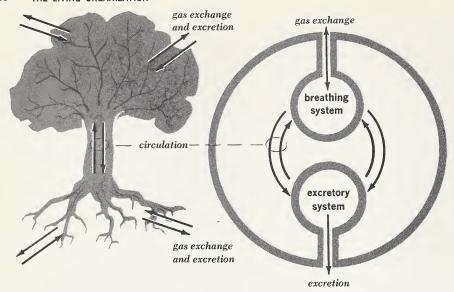
Locomotion and alimentation also greatly influence the internal structure of animals (Fig. 9.1). In certain respects, animal structure matches that of plants. For example, all animals possess reproductive structures, as do all plants. Also, most animals possess circulatory systems and blood, parts which correspond to the nutrient-carrying xylem and phloem of tracheophytes. However, most other features of animal structure do not have counterparts among plants. For to make alimentation and locomotion at all possible, the animal organization must include a number of structural systems not needed in plants.

Thus no plant possesses structures specialized for the collection of environmental oxygen or for the excretion of metabolic wastes. Yet all but the most simply constructed animals possess both: lungs, gills, moist skins, and other specific body parts for breathing, and kidneys, lungs, gills, sweat glands, and other specific body parts for excretion. The reason for this greater internal elaboration of animals lies in the shape of their bodies and, ultimately, in the requirement of locomotion. The light-requiring, stationary plant is built for maximum surface exposure. Practically all its cells are in direct contact with the external environment, and each cell therefore may collect oxygen and excrete CO2, H2O, and other wastes on its own. By contrast, the moving organism, for obvious mechanical reasons, cannot be built in the ramified shape of a tree but must be constructed far more compactly, for minimum surface exposure. Hence in an animal, most cells cannot be in direct contact with the environment, and this necessitates specialized breathing and excretory systems, operating in conjunction with the internal circulatory system (Fig. 9.2).

Above all, animals do not match plants in structures associated directly with the function of movement. Animals possess muscles, and many also fea-

FIG. 9.1. Diagrammatic representation of the basic structure of a moving animal. This is a hypothetical animal, showing the position and function of various body parts and organs usually encountered in many elongated, worm-shaped types.





plants: ramified design;

animals: compact design;
few cells have direct access to environment

FIG. 9.2. Diagram contrasting the ramified architecture of a plant and the compact architecture of an animal. Because of their respective architectures, the animal does, and the plant does not, require specialized breathing and excretory systems.

ture articulated, movable skeletons. And, also unlike plants, animals possess elaborate equipment for internal coordination. For movement must be readjusted often, in response to rapid changes of external locale brought about by movement. Thus animals possess systems for chemical coordination, such as blood, kidneys, and endocrine glands, and systems for neural coordination, such as sense organs, nerves, and brains.

We may emphasize here that neural activities of all kinds, including even the most sophisticated thinking of man, serve fundamentally and primarily toward the control of muscles and of movement in general. In line with this, a close parallelism exists in the degree of nervous and the degree of locomotor development. Sense organs, nerves, and brain

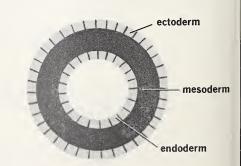


FIG. 9.3. Diagram showing the three germ layers of an animal embryo.

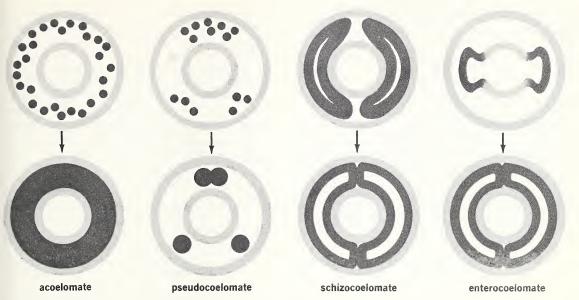


FIG. 9.4. Diagrammatic representation of the formation of mesoderm and the coelom in four animal superphyla. In acoelomates, mesoderm accumulates compactly and a coelom does not develop. In pseudocoelomates, mesoderm accumulates regionally and the body cavity is therefore not a true coelom but is bounded by ectoderm and endoderm. In schizocoelomates, the mesoderm splits into outer and inner layers, and in entro-coelomates, the mesoderm grows out as hollow pouches from the endoderm. In both cases, the end result is the same, namely, a mesoderm-lined, true coelomic body cavity.

centers tend to be greatly reduced in sessile and slow-moving animals, but are highly developed in fast, agile types. For example, the sluggish starfish and sea urchins, though very advanced in other ways, possess but a rudimentary nervous system. So do clams and snails. But their close relatives, the fast squids, possess eyes, nerves, and brains which in structure and efficiency match those of vertebrates.

In general, therefore, just as the plant body reflects a way of life based on photosynthesis and sessilism, so the animal body reflects a way of life based on alimentation and locomotion.

A further point may now be made with regard to animal structure. Broadly speaking, every animal may be considered to be made up of three groups of tissue layers. Each group of layers forms a "tube" of a sort, and the three tubes are one within the other. The outermost tube is the external body wall, which includes the skin and all skin derivatives. The innermost tube is the alimentary tract and its derivatives. And the middle tube consists of all the other tissues and organs between body wall and alimentary tract (Fig. 9.1). This is more than a rough analogy; the three-layered picture of an animal has biological reality. For at an early stage of embryonic life, animal embryos consist of just three single-celled layers. How this stage develops we shall discuss in Chap. 21. Here we may note that the outer embryonic cell layer is called ectoderm, the middle one mesoderm, and the inner one endo-

derm. These three cell layers later produce the three "tubes" of the adult animal. Ectoderm forms the outer tube of skin, nervous system, and other structures. Mesoderm forms the middle tube of muscles, bones, circulatory system, excretory and reproductive systems, and others. And endoderm forms the inner tube of the alimentary system and associated structures (Fig. 9.3).

In the embryo, the three cell layers do not develop at the same time; the middle layer, mesoderm, forms last. In certain animal embryos this mesoderm arises from cells produced by the ectoderm; in other animals, from cells produced by the endoderm; and in still other animals, from cells produced by both ectoderm and endoderm. Further, once the mesoderm is present, it may undergo several later fates. In one series of cases, it expands and develops a large cavity within it. Such a cavity, surrounded entirely by mesoderm cells, is called a coelom. In cases where a coelom forms, it becomes the principal body cavity of the animal. In man, for example, the coelom in part is the cavity inside the abdomen, in which many organs lie (Fig. 9.4).

On the basis of how mesoderm forms and how it develops later, and also on the basis of other structural features, animals can be classified into phyla and superphyla. The superphylum will be our broad unit of discussion, and within each we shall pick one or two representative phyla for more detailed attention.

RADIATA

Phylum PORIFERA: sponges (15,000 species) Phylum CNIDERIA: coelenterates (10,000 species) Phylum CTENOPHORA: comb jellies (100 species)

As the name "Radiata" indicates, the distinguish-

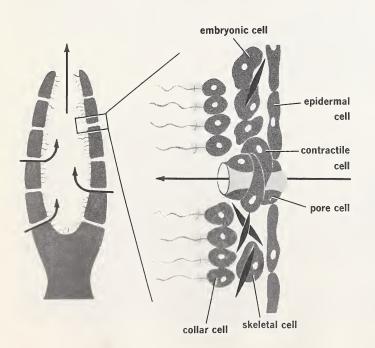


FIG. 9.5. The organization of a simple sponge (diagrammatic). Left: cross-sectional view showing the flow direction of water. Right: detail of a portion of the body wall.

ing feature of this superphylum is a basic *radial* body symmetry. All other animals, by contrast, are basically bilaterally symmetrical, and they are often referred to collectively as "Bilateria."

The Radiata typically possess an alimentary system with but a *single* opening to the outside. The system is essentially a sac, and its one opening serves as both mouth and anus. The mesoderm in this group is not very well developed; in extreme cases it may even be absent altogether (e.g., *Hydra*). Where it does exist it is formed from ectoderm and consists largely of a solid mass of jelly within which are embedded relatively few cells.

Of the three phyla included in the Radiata, we shall discuss only the first two listed above.

Sponges

Class Calcarea: chalk sponges

Class Hexactinellida: glass sponges Class Demispongiae: horn sponges

All sponges are sessile as adults, but their embryos are ciliated and free-swimming. The embryos are essentially saclike, composed of two cell layers, the ectoderm and the endoderm. Jelly often forms a middle layer. When the embryos settle and become adult sponges, the neatly layered arrangement of the cells becomes greatly obscured. Nevertheless, the adults possess different cell types on the outside, the inside, and the middle (Fig. 9.5).

The outer cells are of several kinds, the most distinctive being those which secrete the intracellular spicules, or skeletal elements. These have different characteristic shapes in different species, and they are the basis of sponge classification. In chalk sponges, the spicules consist of calcium salts; in glass sponges, of silica; and in horny sponges, of complex organic materials (Fig. 9.6).

The most characteristic cells on the inside of a sponge are the so-called collar cells, which are flagellate and remarkably resemble the collar flagellates of the protozoan phylum of zooflagellates. These cells line a system of interconnecting channels, which communicate with the environment through entry and exit pores located on the surface

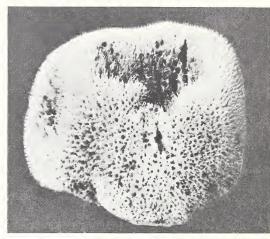
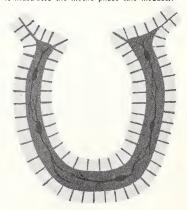


FIG. 9.6. The horny skeleton of a toilet sponge. This quite complex structure was formed by cooperating skeletal cells, each contributing a tiny bit to the mesh of horny fibers. (U.S. Fish and Wildlife Service.)

FIG. 9.7. The basic structure of coelenterates (diagrammatic). The outer body layer is epidermal, the inner is digestive, and the middle one, the so-called mesogloea, is largely jelly in which is embedded a simple nerve net. A single opening serves as both mouth and anus, and there are usually tentacles around this opening. The sessile phase of a coelenterate (the polyp) is as shown, and if the diagram is viewed upside down, it illustrates the motile phase (the medusa).



of the sponge body. The collar cells create a water current which flows through the entry pores into the channel system and out through the exit pores. Food present in the current is trapped by the collar cells (Fig. 9.5).

All sponges are aquatic, and most of them are marine.

Coelenterates

Class Anthozoa: sea anemones, corals Class Scyphozoa: jellyfishes Class Hydrozoa Obelia, Hydra, Physalia

Coelenterates are characterized by a digestive cavity with a single opening, by tentacles which surround this opening, and by sting cells, unique to this phylum, located on the tentacles. The body wall consists of an outer ectodermal cell layer containing sensory cells of various sorts and an inner endodermal layer containing digestive ameboid cells. Between these two cell layers is a jellylike secretion of varying thickness, the mesogloea. In this secretion is embedded a simply constructed nerve net (Fig. 9.7).

The adult coelenterate is either a sessile polyp or a free-swimming, bell-shaped medusa. Hydrozoa

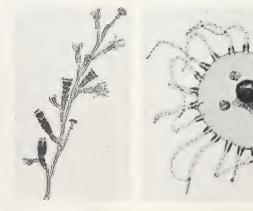
characteristically pass through alternate polyp and medusa stages. In *Obelia*, for example, the sessile phase is a colony of feeding polyps. Such a colony also forms a number of specialized reproductive polyps, which produce medusae by budding. These medusae separate away as free-swimming stages. Eventually they develop sex organs, and after fertilization, the egg develops and gives rise to a new polyp colony (Fig. 9.8).

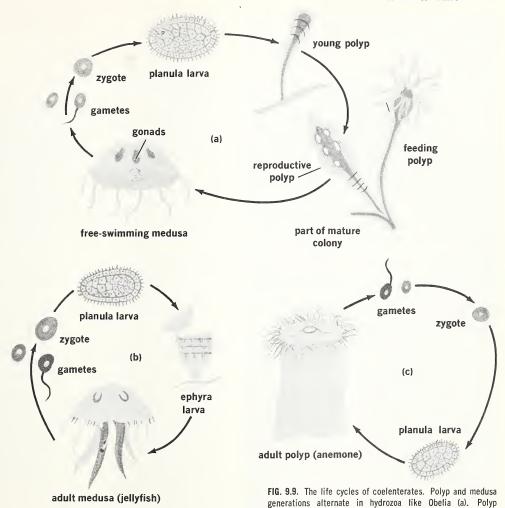
In Scyphozoa, the polyp phase is greatly reduced. For example, in the common jellyfish Aurelia, the fertilized egg grows directly into a single reproductive polyp which buds off medusae. These develop sex organs and give rise to new fertilized eggs.

In *Anthozoa*, on the contrary, it is the medusa phase which is reduced, and indeed that phase is absent altogether: the sessile adult is a feeding polyp which develops sex organs. After fertilization the egg grows into a new adult polyp (Fig. 9.9).

Whether sessile or free-swimming, coelenterates are efficient carnivores which catch crustacea, small fish, and other prey by means of tentacles and sting cells. Most genera are marine, but some, like the familiar Hydra, live in fresh water (Fig. 21.1). Note that Hydra is a highly specialized form in which

FIG. 9.8. The coelenterate Obelia. Left: a colony of polyps. Note feeding polyps with tentacles and club-shaped reproductive polyps. Right: a medusa. Dark region in center is the mouth. Note the four sex organs. (Carolina Biological Supply Co.)





the characteristic hydrozoan life cycle does not occur. In particular, a medusa phase is suppressed. Hydrozoa also include specialized colonial types like *Physalia*, the Portuguese man-of-war, characterized by several different kinds of polyps of distinct form and function (Fig. 9.10). Anthozoa

phases are suppressed in scyphozoa like Aurelia and other jellyfish (b). Medusa phases are suppressed in anthozoa like sea anemones (c).

manufacture often very elaborate exoskeletons of calcium salts, and the group includes the builders of coral reefs and atolls.



FIG. 9.10. Model of Physalia, the Portuguese man-of-war. Each tentacle suspended from the gas-filled float represents a portion of a single coelenterate individual. The several different types of tentacles here indicate the high degree of individual variation encountered in this colony. Other coelenterates are shown in Figs. 19.9 and 21.1. (American Museum of Natural History.)

ACOELOMATES

Phylum PLATYHELMINTHES: flatworms (10,000 species)

Phylum NEMERTINEA: proboscis worms (600 species)

Phylum ACANTHOCEPHALA: spiny-headed worms (300 species)

This superphylum (and all subsequent ones as well) contains bilaterally symmetrical animals. The mesoderm here develops from the ectoderm, and it remains a solid layer (Fig. 9.4). Therefore, because a coelom cavity does *not* form, the name of the group is "acoelomates," i.e., "without coelom."

Of the three phyla included, we shall discuss only the first listed above.

Flatworms

Class Turbellaria: free-living flatworms

Class Trematoda: flukes Class Cestoda: tapeworms

As a group, flatworms are distinguished by a body flattened top to bottom and by a digestive system which resembles that of coelenterates; that is, a single opening (on the underside of the body) serves as both mouth and anus. Note, however, that all other accelemate phyla, and indeed all other animals of any kind, possess alimentary tracts with two separate openings, i.e., separate mouth and anus.

The most familiar free-living flatworms are the planarians (Fig. 9.11). The body of these animals has definite front and rear ends, and the digestive opening is located in the middle, on the underside. An eversible pharynx breaks larger food into particles suitable for ingestion. A pair of eyes is present at the head end, and the head also contains a concentration of nervous tissue, the brain ganglion. From it lead a pair of ventral nerve cords, which are interconnected at more or less regular intervals by transverse strands of nerves. The whole has the appearance of a ladder (Fig. 9.11). Circulatory and breathing systems are not present in flatworms, but planarians possess excretory and elaborate reproduc-

tive systems. Locomotion is accomplished by undulating muscular movements which result in swimming, or by the beat of cilia on the underside of the body, which propel the animal on a solid surface.

The class *Turbellaria*, to which the planarians belong, contains largely free-living scavengers found in both ocean and fresh water. The two remaining classes of flatworms are exclusively parasitic and of considerable general importance to man. We have already discussed the characteristic life cycle in one of these classes (tapeworms) in Chap. 4.

PSEUDOCOELOMATES folse wellow

Phylum ROTIFERA: rotifers (1,500 species)
Phylum NEMATODA: roundworms (10,000 species)

Phylum NEMATOMORPHA: hairworms (80 species)

Phylum GASTROTRICHA (200 species)
Phylum KINORHYNCHA (30 species)
Phylum PRIAPULIDA (3 species)
Phylum ENTOPROCTA (60 species)

In this superphylum, the mesoderm arises largely from ectoderm and it does not become a solid middle layer. Instead, mesodermal tissues collect in limited regions in the space between ectoderm and endoderm. As a result, these animals do possess a body cavity, but this cavity is enclosed by ectoderm on the outside and by endoderm on the inside, not by mesoderm (Fig. 9.4). The cavity is therefore a "false coelom," hence the name "pseudocoelomates."

Another characteristic of the superphylum is that the cells of the adults in many cases lose their bounding plasma membranes, and the animals so become syncytial. With one exception (Entoprocta), the phyla in the group comprise worm-shaped animals, and most of them exhibit a tendency toward superficial external body segmentation. Pseudocoelomates as a whole include some of the rarest and least known, as well as some of the most abundant, of all animals. We shall describe the first two of the seven phyla listed above.

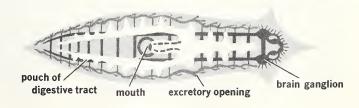
Rotifers (all deserts)

These microscopic animals are very largely freeliving, and they are found predominantly in fresh water, where they are exceedingly common.

They possess an identifying anterior crown of cilia surrounding the mouth, hence the name "wheel bearers" for the phylum. The cilia are the organs of locomotion, and they also create food currents. The mouth leads into a muscular grinding

FIG. 9.11. Free-living planarian flatworms. External view, slightly larger than natural size; internal structure diagrammatic. (Photo, Carolina Biological Supply Co.)





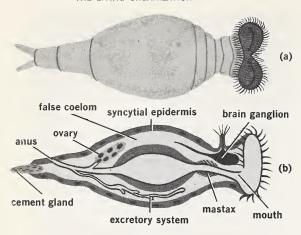


FIG. 9.12. The structure of a rotifer, diagrammatic. (a) Dorsal external view. (b) Sagittal section.

organ, the mastax, and then into a straight intestine which terminates at the anus. At the hind end are located cement organs, which anchor the animal during feeding and which also make possible a second form of locomotion resembling caterpillar-like creeping. The nervous system consists mainly of a brain ganglion dorsal to the mouth and of a series of nerve cords leading away from it. Rotifers possess excretory systems, but circulatory and breathing systems are absent (Fig. 9.12).

One of the long-known peculiarities of these animals is that the number of cells in late embryos, and the number of nuclei in adults, is constant for each species. Also, the nuclei occupy fixed positions in each individual. The body plan of each species may thus be mapped out nucleus by nucleus.

During spring and summer, female rotifers produce eggs which develop into new females without being fertilized. These females in turn reproduce without fertilization, and many generations of females succeed one another in this manner. In the fall, the females lay some eggs which are smaller

than the rest. These hatch into small males, degenerate individuals lacking digestive systems but capable of producing sperms. Fertilization may then occur. The resulting eggs possess thick, hard shells and may resist unfavorable environments for very long periods. Under suitably favorable conditions, for example, in the following spring, the shelled eggs develop into females. In some types of rotifers males are unknown altogether, the species being propagated exclusively by unfertilized eggs. This phenomenon of egg development without fertilization is called parthenogenesis. We have already encountered it in the discussion on social insects (Chap. 4).

Roundworms

It has been estimated that probably more individual roundworms exist than any other animals except possibly insects. Many nematodes are free-living in soil and water, and they occur in such numbers that a spadeful of garden earth is likely to contain up to a million worms. Many nematodes are parasitic in plants and animals, and they are usually implicated when an animal is said to suffer from "worms." Man alone harbors some 50 species. Most of these are relatively harmless, but some cause serious diseases (Fig. 9.13).

All nematodes are remarkably alike. The body is slender and cylindrical, with tapered ends, and is covered with a tough chitinous cuticle. Males are usually smaller than females. As in rotifers, the number of nuclei is constant for each species and cell boundaries are absent in the adult. The worms possess mouth, straight intestine, and anus. Circulatory and breathing systems are not present.

Among the serious nematode pests of man are the *trichina worms*, introduced into the human body via insufficiently cooked pork; the *hookworms*, which live in soil and infect man by boring through his skin; and the *filaria worms*, which are transmitted by mosquitoes and cause blocks in lymph vessels. The disease resulting from filarial infections is characterized by immense swellings and is known as *elephantiasis*.

SCHIZOCOELOMATES

Phylum MOLLUSCA: mollusks (100,000 species) Phylum ANNELIDA: segmented worms (10,000

species)

Phylum ARTHROPODA: joint-legged animals

(1 million species)

Phylum SIPUNCULOIDEA (250 species)

Phylum PHORONIDEA (15 species) Phylum ECHIUROIDEA (60 species)

Phylum ECTOPROCTA (2,500 species)

In this enormous superphylum, the mesoderm has two sources. The mesoderm of the embryo forms from ectoderm but later largely degenerates. New adult mesoderm, developed from endoderm, later splits into two layers, an outer one which comes to lie against the inner surface of the body wall and an inner one which surrounds the alimentary tract (Fig. 9.4). Thus the animals have a true coelom, and since it arises by a splitting of mesoderm, the group is named "schizocoelomates."

Mollusks

Class Amphineura: chitons Class Scaphopoda: tooth shells

Class Gastropoda: snails, slugs, whelks Class Pelecypoda: clams, mussels

Class Cephalopoda: squids, octopuses, nautiluses

Among Metazoa, this enormous phylum is second only to the arthropods in numbers of species. Mollusks are mostly marine, but many snails and clams live in fresh water and one group of snails is terrestrial. Mollusks are exceedingly abundant in all aquatic habitats. As a group, they illustrate the general principle that successful phyla are highly diversified in structural adaptations and ways of life. We may note too that the phylum includes the largest of all nonvertebrate animals, namely, the giant squids, which may reach lengths of 50 ft.

Despite the external dissimilarities of the members of different classes, all mollusks share a common fundamental body organization. The molluscan body consists of a ventral, muscular foot, which

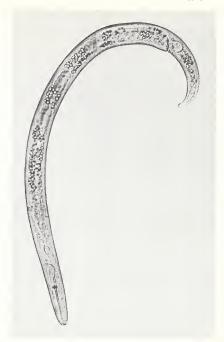


FIG. 9.13. A mature female of the nematode Paratylenchus, which causes disease in plants. (Courtesy of Dr. W. F. Mai, Cornell University.)

is the principal organ of locomotion; a visceral mass, located dorsal to the foot, which contains most of the internal organs; and a mantle, a tissue layer which covers the visceral mass and which in most cases secretes a calcareous shell (Fig. 9.14).

The class Amphineura includes probably the least specialized mollusks. Chitons occur abundantly on rocks along the seashore, where they creep sluggishly with their broad foot. The dorsal surface of a chiton is protected by a shell of eight overlapping plates, and under the rim of this shell, in the so-called mantle cavity, are lateral gills for breathing. Between shell and foot is the visceral mass. The head is greatly reduced, probably a specialized feature of chitons (Fig. 9.15).

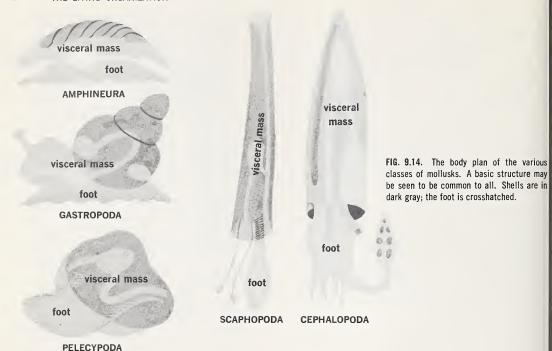


FIG. 9.15. A chiton, seen from the dorsal side. Note the eight shell plates and the edge of the foot. (American Museum of Natural History.)



In the class *Scaphopoda*, the body is elongated in a dorsoventral direction and the animal is tubular. The shell is a tube open at both ends, and the foot of a scaphopod protrudes from the wider ventral end. Scaphopods are the least common of the mollusks. They are all marine, and they live partly buried in sand or mud boftoms of shallow waters.

Gastropoda like snails have the general architecture of chitons. A distinct head is present, however, which bears retractile tentacles and eyes. Also, the shell is usually coiled and the head and foot of the animal may be withdrawn into the shell. The alimentary tract is U-shaped, and the anus opens to the outside dorsally, under the forward rim of the shell. Aquatic snails breathe by means of gills, located as in chitons in the mantle cavity, under the rim of the shell. In terrestrial snails, parts of

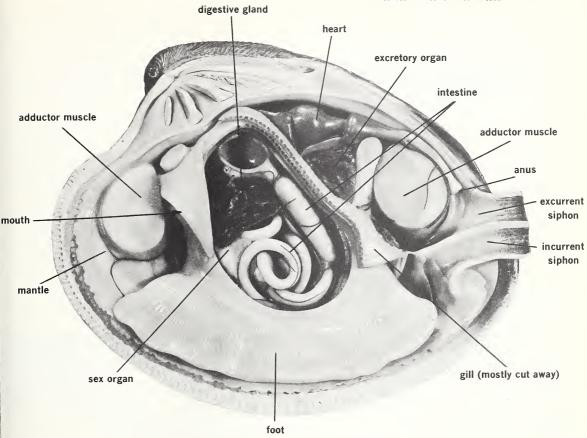


FIG. 9.16. The internal structure of a clam. In this model, most of the gill flap is cut away, to expose the organs of the visceral mass. Water enters via the incurrent siphon and passes over the gills, where food particles are strained out and conducted to the mouth, hidden under a flap of tissue. Water and elimination products of all kinds leave the clam via the excurrent siphon. The two adductor muscles control the closing of the valve shells. (American Museum of Natural History.)

the mantle cavity have become adapted to function as lungs. Some land snails have returned secondarily to water, and these must surface periodically for air.

In the class *Pelecypoda*, clams are highly specialized animals, adapted to a burrowing way of life

(Fig. 9.16). They are flattened from side to side, the hinge of the two shells, or valves, being dorsal.

Lining the valves on the inside are the mantle tissues, which form two openings at the posterior end, one for the entry and one for the exit of water.



FIG. 9.17. A horse clam, showing the extensible tube containing the incurrent and excurrent siphons. When the animal is deeply embedded in mud or sand, the siphon tube may be extended upward into clear water. (Courtesy of V. B. Scheffer, U.S. Fish and Wildlife Service.)



In many species, these posterior tissues are drawn out into a long retractile tube, which may be pushed out into free water if the clam is embedded in several inches of sand or mud (Fig. 9.17). Hanging freely into the mantle cavity are the gills, folds of ciliated tissue which function both as breathing organs and as food filters. Pelecypods subsist on microscopic food particles brought into the animals by the incoming water current. The gills strain and collect these particles, and the cilia carry them to the mouth. This opening is located anteriorly between the left and right gills, in the visceral mass. The digestive tract is within the visceral mass, and the anus opens posteriorly, discharging into the outgoing water current. The nervous system is highly reduced, a feature undoubtedly correlated with the sluggish way of life of these animals. A head is not present either. The muscular foot, continuous with the visceral mass, may be protruded between the valves. Clams use the foot as a burrowing organ, and by expanding the tip of the foot in sand and pulling the body after it, they may propel



FIG. 9.18. Cephalopod mollusks. (a) An octopus. (b) The chambered nautilus. A section through the shell is also shown. (American Museum of Natural History.)

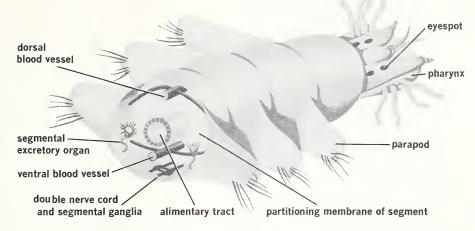


FIG. 9.19. Anterior part of the polychaete Nereis, and cross section through the body (diagrammatic).

themselves forward. Many pelecypods are permanently attached, however. This is true, for example, of oysters, and also of the giant clam *Tridacna*, which may be 2 yd long and weigh ½ ton.

The class *Cephalopoda* includes the most highly organized mollusks (Fig. 9.18). Squids have a greatly reduced horny shell embedded within the mantle. Octopuses are without shells. Cephalopods are elongated dorsoventrally, like scaphopods. In squids, the sucker-equipped tentacles represent the foot, and the body represents the visceral mass (Fig. 9.14). Within the wreath of tentacles is a well-developed head, with a large brain and large vertebratelike eyes. The head also bears a mouth which is equipped with strong horny jaws. The digestive tract is Ushaped, the anus opening into the mantle cavity. Cephalopods are marine, predatory animals.

Segmented worms

Class Polychaeta: sandworms, clamworms, tube worms

Class Oligochaeta: earthworms Class Hirudinea: leeches This phylum comprises animals in which the body is divided internally and externally into numerous segments, separated from each other by membranous partitions. Except for the segments of the head and the hind end, all others are more or less alike. The digestive, nervous, and circulatory systems run uninterruptedly from front to rear, but all other organs are arranged on a segmental basis (Fig. 9.19).

The first three segments of an annelid form the head, and the last segment represents the hind end. The mouth, located anteriorly in the head, leads into an alimentary tract which terminates in the last segment. The head also contains the brain ganglia, which form a ring around the pharynx. The rest of the nervous system is essentially of the ladder type, consisting of ventral nerve trunks thickened into ganglia in each segment. The circulatory system is composed principally of a longitudinal dorsal vessel, a longitudinal ventral vessel, and segmental connecting channels between these two. Blood flows forward dorsally and backward ventrally, propelled mainly by contractions of the

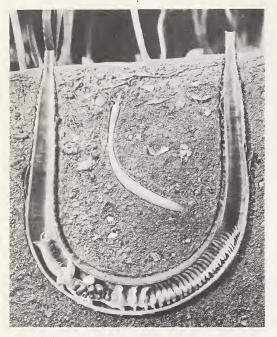


FIG. 9.20. Polychaetes. Section through the tube of the parchment worm Chaetopterus. The head of the worm is on the left. Note the greatly elaborated parapodia, used to draw water currents through the tube. Between the arms of the U tube is a sipunculid worm, a member of another phylum. (American Museum of Natural History.)

dorsal blood vessel. A pair of excretory organs with separate openings is found in each body segment. The cuticle-covered body surface of an annelid serves for breathing.

The *Polychaeta* (Fig. 9.20) form the largest and probably the most primitive class. These worms are mostly marine. Some are free-swimming. Others manufacture tubes in mud or sand in which they live permanently. And still others are burrowers. All are distinguished by the presence of a pair of fleshy, bristle-studded lobes, the **parapodia**, on each body segment (Fig. 9.19). These lobes provide a

large surface for breathing, and their beating also aids in locomotion or in drawing water in and out of tubes and burrows. Polychaetes are characterized further by the presence of eyes, and of other specialized sense organs in the head segments.

The Oligochaeta include the familiar earthworms. Annelids of this class differ from polychaetes in the absence of eyes and other head appendages, and in the absence of parapodia, each body segment bearing only a few bristles. Oligochaetes live in the ocean, in fresh water, and on land. Some attain remarkable size. For example, the giant earthworms of Australia may reach lengths of over 10 ft and diameters of several inches.

The Hirudinea, or leeches, are without bristles, and unlike other annelids, they possess a fixed number of segments throughout life. Moreover, the external segmentation does not match the internal, external segments being the more numerous. Each end of the body is equipped with a sucker. The most familiar leeches are blood-sucking ectoparasites. These possess digestive tracts equipped with spacious pouches, which may store enough blood to make a single meal suffice for many months. The worms produce hirudin, an anticoagulant which prevents blood from clotting during ingestion.

The segmentation of annelids is a trait of considerable adaptive advantage. It permits the development of different specializations in different segments, just as, on a lower level of organization, division of protoplasm into cells makes possible divergent cellular specializations. In modern annelids such divergent segmental specialization has not proceeded very far and most segments are still rather alike. However, the inherent possibilities were exploited to the utmost in another phylum, which, we are fairly sure, evolved from primitive annelid stock: the arthropods.

Arthropods

Class Onychophora Peripatus

Class Ćrustacea: shrimps, lobsters, crabs, barnacles Class Insecta: insects Class Chilopoda: centipedes Class Diplopoda: millipedes

Class Arachaida: spiders, scorpions, mites, ticks

Class Merostomata: horseshoe crabs

By any standard, this is today the most successful group of organisms in the whole living world. Arthropods are encountered in all environments in which life occurs at all, and in many tropical environments they maintain supremacy over even man. The insects are by far the most abundant and most diversified of all arthropods, being represented in the phylum by at least three-quarters of a million species.

General characteristics. The body plan of arthropods as a whole is a highly elaborated variant of that of annelid worms (Fig. 9.21). A segmented design is fundamental, and the different segments are specialized in often greatly divergent ways. The

body of an arthropod is composed of a head, a thorax, and an abdomen. The whole is covered by an external skeleton made of chitin. This skeleton is shed, or molted, at intervals, and a new skeleton then develops. Jointed appendages are present on most or all segments.

The head consists of six segments. Fused together in the adult, each head segment characteristically bears a pair of appendages having either a sensory or an ingestive function. The head in addition contains so-called simple eyes, and in most cases also compound eyes. In the latter, many complete visual units are grouped together into large composite types of eyes with many lenses. Such compound eyes are unique to arthropods.

The alimentary tract consists of foregut, midgut, and hind gut. The first and last of these sections are lined with chitin. Hence only the midgut functions digestively. Nervous structures include dorsal brain

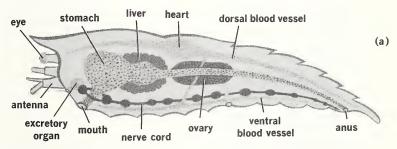
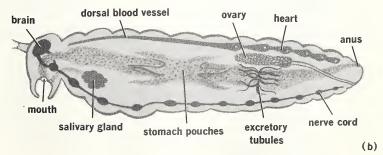


FIG. 9.21. The internal structure of a lobster (a) and a grasshopper (b); diagrammatic.



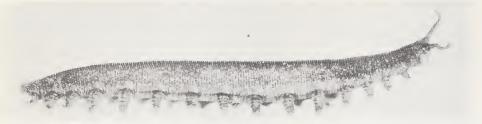




FIG. 9.22. Peripatus. This animal combines annelid and arthropod features. Among the annelid features are the general body shape, the head of three segments, the fleshy, parapodialike, unjointed legs, the segmental excretory organs, and the ciliated reproductive tracts. Among arthropod features are the antennae, the claws on the legs, the tracheal tubes for breathing, and the open blood circulation. (Carolina Biological Supply Co.)

ganglia in the head, ventral nerve cords, and paired ganglia either in each segment or grouped together in head and thorax. The circulatory system consists of a single dorsal vessel. Blood flows out from it anteriorly, circulates freely through the body tissues, and reenters the vessel posteriorly. The excretory organs are located either in the head appendages, as in crustaceans, or, as in insects, they are attached to the midgut and lead to the outside via the anus.

Breathing is accomplished in various ways in the different groups. Aquatic arthropods typically possess gills of some kind. In lobsters, for example, feathery gills are attached to the upper parts of the walking legs. Terrestrial arthropods like insects breathe by means of tracheal tubes, unique, chitinlined systems of channels which originate on the body surface and ramify to all interior tissues.

The fertilized eggs of many aquatic arthropods develop into free-swimming larvae. These resemble annelid worms to a considerable extent. This is true

FIG. 9.23. Dorsal view of a crayfish, a fresh-water crustacean structurally very much like the marine lobster. Note the antennae, eyes, large claws, walking legs, uropods, and telson. The fused cephalothorax, covered by the carapace, is clearly set off from the abdominal segments. (Carolina Biological Supply Co.)

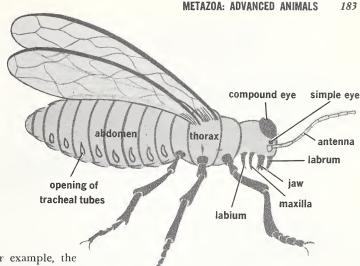


FIG. 9.24. The external structure of an insect.

also for some terrestrial larvae, for example, the insect caterpillars. In other arthropods, an annelid-like larval stage does not occur and when the larvae hatch they already look like miniature adults. All larval types develop through a series of molting steps, the last of which produces the adult. Insects do not molt after adulthood is attained, but crustaceans do molt throughout life.

Class characteristics. The members of the small class Onychophora indicate strikingly the close relation between annelids and arthropods. Peripatus, for example, features an interesting and unique mixture of annelid and arthropod traits (Fig. 9.22). It is believed that Onychophora are remnants of an evolutionary line which branched off the ancestral arthropod stock, very soon after that stock itself had evolved from annelid ancestors.

The large class of *Crustacea* is represented by some 50,000 species. Most crustaceans are aquatic, and most of these are marine. Many are microscopic and planktonic, but others, like the giant crabs, may be some 12 ft across from one leg tip to the other. Most crustaceans are free-living and free-swimming. But some are parasitic either as larvae or as adults, and the barnacles are sessile as adults. In their internal structure, crustacea display a typically

arthropod organization (Fig. 9.21). Externally, they show particularly clearly how different segments may become specialized for different functions; consider, for example, the pronounced differences among the segmental appendages of a lobster (Fig. 9.23).

In the class *Insecta*, largest of all animal groups, the head is marked off clearly from the thorax, and the thorax from the abdomen (Fig. 9.24). The head bears simple and compound eyes, a single pair of antennae, and mouth parts which vary according to how the insect feeds: by *biting* like a grasshopper, by *sucking* like a housefly, or by *piercing and sucking* like a mosquito.

The thorax consists of three segments, each bearing a pair of walking legs. Also, in all except the most primitive insects, which are flightless, and secondarily flightless insects like fleas, each of the last two thoracic segments typically bears a pair of wings. Both pairs may be membranous, as in dragonflies and butterflies. Or the first pair may be heavily chitinized, as in beetles. Or the second pair may be reduced to tiny stalks, as in houseflies and mosquitoes. The abdomen of insects characteristically is without appendages.

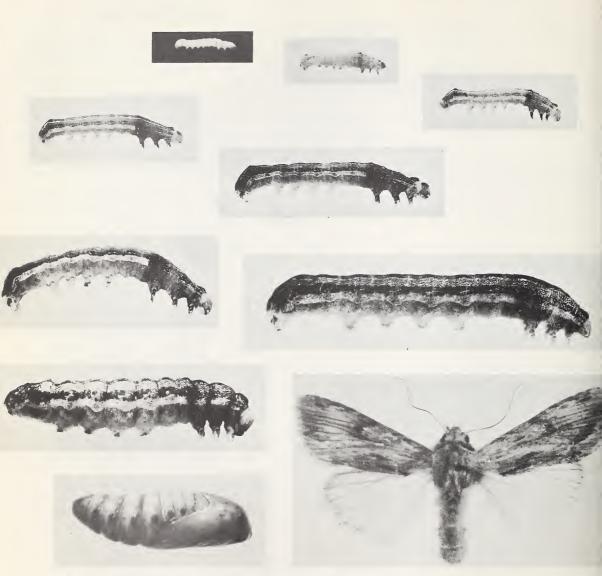


FIG. 9.25. Complete metamorphosis in insects. Note, top left to bottom right, the successive annelidlike larval stages (caterpillars), the pupa (next-to-last stage), and the winged adult stage. Each stage is connected to the preceding and succeeding one through a molt. In insects with incomplete metamorphosis, the larvae look like miniature adults. (Courtesy of Dr. D. Bodenstein, Gerontology Branch, Baltimore City Hospitals.)

Insects become adults either by incomplete or by complete metamorphosis. In the former, the larva resembles the adult in general features and reaches the adult condition gradually, in the course of usually five molting steps. Grasshoppers, earwigs, termites, true bugs, aphids, and many other insect types belong to this group. In the second case, the larva is annelid- or caterpillarlike. It eventually transforms into a pupa, and the pupa in turn becomes the adult. Butterflies, moths, houseflies, beetles, bees, and ants are in this group. In both groups, we may note, only the adult stages fly (Fig. 9.25).

Insects are classified into some 20 orders, each representing a very wide range of ways of life. For example, the order of beetles includes parasites, commensals, carnivores, herbivores, omnivores, aquatic types, subterranean types, arboreal types, diurnal and nocturnal types, and dozens of others, each adapted to a particular, often highly specialized mode of living. Analogous diversity is in evidence within most other orders. We may note, incidentally, that beetles alone number some 300,000 species, and they form the largest of all orders, within the largest of all classes, within the largest of all phyla.

The classes Chilopoda and Diplopoda (Fig. 9.26) are exclusively terrestrial. Centipedes and millipedes resemble each other in many ways, but they are nevertheless sufficiently distinct to be ranked as separate classes. In both groups, the rather wormlike animals are subdivided into numerous segments. In the head, simple eyes are present but compound eyes usually are not. Body segments bear walking legs, one pair per segment in centipedes, two pairs per segment in millipedes. The first pair in centipedes is modified into poison claws. Centipedes are carnivorous, whereas millipedes are largely herbivorous. Despite the comparatively greater number of legs in millipedes, these arthropods cannot run as fast as centipedes. In their general internal structure, centipedes and millipedes are rather like insects.

The classes Arachnida and Merostomata are



FIG. 9.26. (a) A centipede. (b) A millipede. Note the two pairs of legs per segment in millipedes, the single pair per segment in centipedes. (Carolina Biological Supply Co.)

(b)

related rather closely. Arachnids comprise terrestrial arthropods. The head in these animals is without compound eyes and without antennae. In spiders, the head bears sharp-pointed poison-injecting claws. On the thorax are four pairs of walking legs, and this feature readily distinguishes spiders, and arachnids generally, from insects. The abdomen is without segmental appendages, but spiders possess several pairs of posterior spinnerets, organs which secrete web-forming silk.

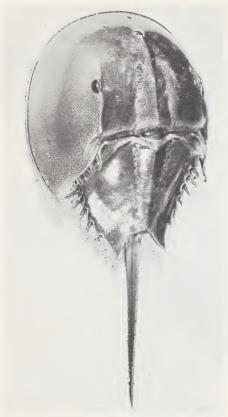


FIG. 9.27. The horseshoe crab Limulus. This arthropod may be regarded as a "living fossil," having persisted more or less unchanged for 200 million years or more. (Carolina Biological Supply Co.)

The Merostomata are the marine horseshoe crabs, or *king crabs*. These are represented by five living species, all belonging to the genus *Limulus* (Fig. 9.27). The animals are archaic "living fossils," and they probably are survivors of an early branch of the aquatic stock which also gave rise to the modern arachnids.

ENTEROCOELOMATES

Phylum BRACHIOPODA: lampshells (250 species)

Phylum CHAETOGNATHA: arrowworms (30

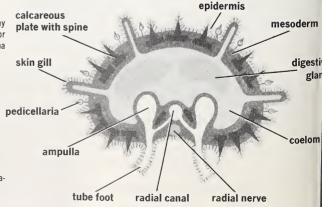
Phylum POGONOPHORA: beard worms (25 species)

Phylum HEMICHORDATA: acorn worms (100 species)

Phylum ECHINODERMATA: spiny-skinned animals (6,000 species)

Phylum CHORDATA: chordates (50,000 species)

Mesoderm in this superphylum arises exclusively from endoderm. At an early embryonic stage, the endoderm produces hollow pouches which grow into the space between ectoderm and endoderm. Eventually these pouches fill the entire available space, and they also separate off from the endoderm



 ${\sf FIG.~9.28.}$ Cross section through the arm of a starfish; diagrammatic.

which produced them. The cavities, so enclosed completely by the mesodermal pouches, are the coelom (Fig. 9.4). Since the mesoderm and coelom here arise from the endoderm, which itself produces the gut (or *enteron*), the group is named "enterocoelomates."

Of the six phyla included, we shall discuss only the last two listed above. The last is undoubtedly of very special interest, for man and the other mammals belong to it.

Echinoderms

Class Asteroidea: starfishes Class Ophiuroidea: brittle stars

Class Echinoidea: sea urchins, sand dollars

Class Holothuroidea: sea cucumbers Class Crinoidea: sea lilies, feather stars

The members of this phylum are exclusively marine, and their unique identifying feature is a so-called water-vascular system for locomotion. The embryos and larvae are bilateral, but the adults are radially symmetrical.

A starfish of the familiar genus Asterias is composed of a central region from which five arms radiate out. In other genera, there may be as many as 20 or more arms. The shell-like skeleton is made up of small flat calcareous plates (Fig. 9.28). Short calcareous spines, some of them movable, project from the skeletal plates. Covering the skeleton are epidermal tissues, which are studded with many tiny fingerlike protrusions, the skin gills. The internal cavities of these gills are parts of the coelom, and they communicate with the interior body cavity through spaces left among the skeletal plates. Also present on the body surface are numerous very small pincers, the pedicellariae. These protect the skin gills from interference by small animals.

The water-vascular system communicates with the outside through a madreporite, a sievelike device located excentrically on the upper surface of the animal (Figs. 9.29 and 9.30). A series of ducts leads from the madreporite to the hollow, muscular tube feet, which project from the underside of the arms. At the base of each tube foot is a muscular

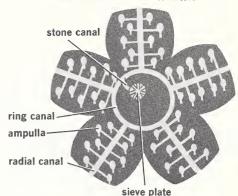


FIG. 9.29. The components and the internal arrangement of the water-vascular system in a starfish. Water enters and leaves the system through the sievelike madreporite (sieve plate) at the upper side.

sac, which may force water into the foot and so make it stiff (Figs. 9.28 and 9.30).

The mouth is on the undersurface in the center of the body, and in the center of the upper surface is a small anal pore. Connecting mouth and anus is a stomach, into which open five pairs of digestive glands, one pair from each arm. Starfishes feed largely on clams. The tube feet, working in relays, are used as suckers to pull on the valves of a clam until the clam is exhausted and opens its housing. The stomach of the starfish then turns inside out through the mouth and digests the soft tissues of the clam. The nervous system of starfishes consists of a ring of nerve tissue around the mouth, from which nerve trunks radiate into each arm. The circulatory system is also greatly reduced. Excretion is accomplished partly by diffusion, partly by migrating ameboid cells. These are dispersed freely in the body cavity, and they carry wastes to and through the epidermis.

The members of the other echinoderm classes largely resemble starfishes in their general features. Among the brittle stars, the five arms are elongated

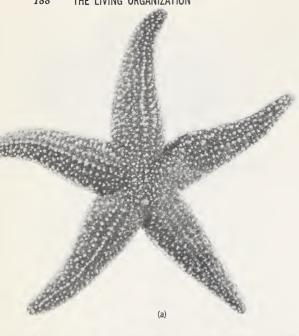




FIG. 9.30. Starfish. (a) View from top. Note the madreporite as a round spot in the angle between the two lower arms. (b) View from below, showing tube feet. [(a) Carolina Biological Supply Co.; (b) Woody Williams, Inverness, Calif.]

and slender and their sinuous movements aid in locomotion. In some ophiuroids the arms are branched. Echinoids are without arms, but their bodies nevertheless are organized on a plan of five or of multiples of five. For example, sea urchins possess five bands of long slender tube feet and a mouth equipped with five radially placed teeth. Long movable spines are characteristic of these animals. The sea cucumbers (Fig. 9.31) are elongated along the mouth-anus axis, and they are further distinguished by a highly reduced skeleton, a leathery body covering, and a circlet of tentacles around the mouth. Five longitudinal bands of tube feet are typical of most members of this class. Crinoids are stalked, sessile, deep-water forms, characterized by numerous feathery arms.

The early embryonic development of echinoderms is quite similar to that of chordates, and there is little doubt that echinoderms and chordates are fairly closely related.

Chordates

Subphylum Urochordata: tunicates Subphylum Cephalochordata: lancelets Subphylum Vertebrata: vertebrates

Class Agnatha: jawless fishes

Class Placoderms: armored fishes (extinct)

Class Chondrichthyes: cartilage fishes

Class Osteichthyes: bony fishes Class Amphibia: amphibians

Class Reptilia: reptiles

Class Aves: birds

Class Mammalia: mammals

Because this phylum includes man and the animals most directly important to man, it is unquestionably the most interesting from almost any standpoint. Chordates as a whole are characterized by the possession of a notochord, a hollow, dorsal nerve cord, and paired gill slits (Fig. 9.32). These structures are present either throughout life or only at some stage of development. The notochord (hence the name "chordate") is a dorsal stiffening rod formed from embryonic mesoderm. The nerve cord and later nervous system form from the em-

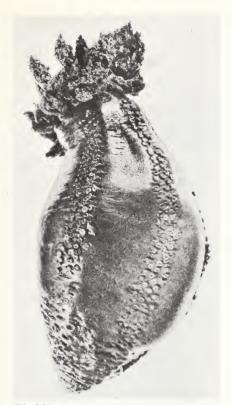


FIG. 9.31. A sea cucumber. Note the leathery skin, the tentacles surrounding the mouth, and the rows of tube feet. (Carolina Biological Supply Co.)

bryonic ectoderm. Gill slits are essentially channels on each side, which connect the exterior of the body with the front part of the alimentary tract, specifically the region behind the mouth called *pharynx*. Thus a continuous water channel is established from the mouth to the pharynx and from the pharynx to the outside through the gill slits. Food present in the water taken in by mouth is collected in the pharynx and is passed on into the esophagus. The water returns to the environment via the gill slits past the gills, where oxygen is absorbed into the circulatory system.

The body is segmented in two of the three chordate subphyla, the lancelets and the vertebrates. This feature is shared in common with the annelidarthropod group of organisms, but it has here evolved independently. A distinct head is present only in vertebrate chordates.

Subphylum Urochordata. Tunicates, or "sea squirts," are marine. Of the approximately 2,000 known species, most are sessile and many form extensive colonies in the water. The adults are quite unlike typical chordates, but their larvae clearly reveal the chordate character of these animals. A tunicate larvae has the general form of a tadpole (Fig. 9.33). It possesses a large muscular tail, a very well developed notochord, and a dorsal hollow nerve cord, expanded anteriorly into a primitive brain. A complete alimentary system is present, as are pharyngeal gill slits.

After a free-swimming existence of some hours,

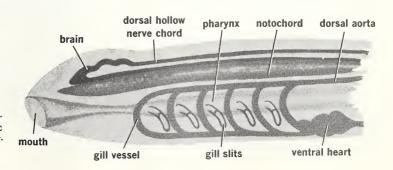
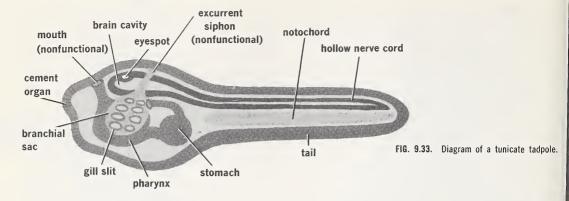


FIG. 9.32. The anterior portion of a hypothetical chordate, to show the basic diagnostic features of the phylum Chordata.



such a larva attaches with its anterior end to a rock or other solid object and undergoes a remarkable transformation. In the adult (Fig. 9.34), the tail is resorbed, the notochord has disappeared completely, and the nervous system has become reduced to a single ganglion. The pharynx has enlarged, however, and has developed many additional gill slits. Also, the region of the mouth has shifted so that the alimentary tract is roughly U-shaped. A cellulosecontaining covering, the tunic, has developed around the whole animal, leaving only two openings, the incurrent and excurrent siphon. Water and food enter the animal via the incurrent opening. Food is filtered out in the pharynx and is carried over a ciliated groove into the esophagus. Water passes through the gill slits and leaves via the excurrent siphon. This opening also conducts waste products to the outside.

It was probably the tadpole stage of ancestral tunicates which gave rise to the other chordate subphyla.

Subphylum Cephalochordata. The lancelets, often better known by the group name amphioxus, comprise some 30 species of small marine sand burrowers. These animals are more or less fish-shaped, slender, and compressed laterally (Fig. 9.35). They possess a notochord which persists throughout life

FIG. 9.34. Cutaway model of an adult tunicate. Food-bearing water is drawn into the pharynx through the incurrent opening. Food passes into the U-shaped alimentary tract, and water emerges through the gill slits and the excurrent opening to the outside. (American Museum of Natural History.)

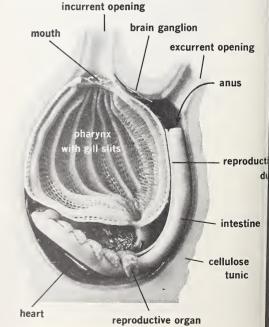


TABLE 6. Some diagnostic features of vertebrates

Super- class	Class	Skin	Skeleton	Append- ages	Breath- ing	Heart chambers	Fertili- zation	Develop- ment	Other
Pisces	Agnatha	Smooth	Permanent notochord plus car- tilage skeleton	Without paired fins	Gills	2	External	In water	Without jaws; cold-blooded; without neck; without lungs
	Chondrich- thyes	Denticles	Embryonic notochord; adult car- tilage skeleton	Paired fins	Gills	2	External	In water	With jaws; cold-blooded; without neck; without lungs
	Osteich- thyes	Scales	Embryonic notochord; adult bony skeleton	Paired fins	Gills; lungs in some	2	External	In water	Swim bladder in most; cold-blooded; without neck
Tetrapoda	Amphibia	Smooth, glan- dular	Embryonic notochord; adult bony skeleton	2 pairs legs	Gills and lungs	3	External	In water	Cold-blooded; without neck
	Reptilia	Scales	Embryonic notochord; adult bony skeleton	2 pairs legs	Lungs	4	Internal	On land	With neck; cold-blooded
	Aves	Feathers	Embryonic notochord; adult bony skeleton	Legs and wings	Lungs	4	Internal	On land	With neck; warm-blooded
	Mammalia	Hair	Embryonic notochord; adult bony skeleton	2 pairs legs	Lungs	4	Internal	Mostly within female	Warm-blooded; nurse young; nonnucleated red corpuscles

and which extends through the whole length of the body. The nerve cord is dorsal and tubular, but there is no brain and a head is not present. The mouth leads into a ciliated pharynx with 60 or more pairs of gill slits. Water passing through these

emerges into an atrium, a chamber which surrounds the pharynx and opens ventrally, anteriorly to the anus.

Amphioxus is a segmented animal. This is shown most obviously by the musculature, which is formed

FIG. 9.35. Amphioxus, the lancelet. The many pharyngeal gill slits are very prominent just behind the mouth. Note also the notochord, the very dark rod just above the gill slits, running from front to back. A head is absent. (Carolina Biological Supply Co.)





FIG. 9.36. Lamprey, lateral view. Note the gill slits. (Carolina Biological Supply Co.)

into segmental bundles, or somites. The nerves leading to these muscles and the excretory and reproductive organs are arranged on a segmental pattern too. Lancelets therefore are clearly, and very closely, related to vertebrates. They differ from vertebrates principally in the permanence of the notochord and in the absence of a head.

Subphylum Vertebrata. The vast majority of chordates are vertebrates, so named because, in later embryonic stages, a segmented vertebral column develops in addition to, or more generally as a replacement of, the notochord. The individual vertebrae are made of cartilage or bone. Segmentation is a general feature of vertebrate structure, but in many groups the segmental patterns become somewhat obscured in adult stages. Vertebrates possess a well-developed head, with brain, brain case, and paired sense organs. The nerve cord is dorsal and tubular, as in other chordates. Pharyngeal gills are present too, and in most groups an outpouching from the pharynx develops into a lung. Gills and lungs rarely occur at the same time, the gills usually forming first, the lungs thereafter. A distinct adult tail is a virtually unique vertebrate characteristic. The base of the tail is marked ventrally by the anus. Some of the identifying characteristics of the seven living classes are as follows (see also Table 6).

Agnatha. These are roughly eel-shaped animals, with smooth, scaleless skin and without paired fins (Fig. 9.36). The anterior end of the body is modified into a funnel-like sucker, in the center of which is the mouth. Jaws are absent. The notochord persists throughout life, and the adult in addition possesses

a brain case and segmental vertebral elements made of cartilage. There are seven pairs of gills, and lungs do not form. The heart is ventral as in all vertebrates, and as in all fishes it consists of two chambers, one auricle and one ventricle. The sense organs include, apart from lateral eyes, a functional pineal eye, located dorsally along the mid-line of the head. Lampreys comprise fresh-water as well as marine species, but even the latter migrate into rivers for spawning.

Chondrichthyes. In this and all subsequent vertebrate classes, the notochord is an embryonic structure only and is replaced completely by a vertebral column. In the chondrichthians, this column and all other skeletal parts consist of cartilage. The class includes sharks, skates, and rays, most of them marine but some living in fresh water. Two pairs of fins are present in addition to several unpaired fins, as are upper and lower jaws, characteristic also of subsequent classes. Breathing is by gills, of which there are five to seven pairs. The cartilage fishes are strongly muscled, and most are active, open-water predators. Some are plankton feeders, and these include the whale sharks, which sometimes reach lengths of approximately 50 ft and are the largest vertebrates after the true whales.

Osteichthyes. At least half the number of all vertebrate species are bony fishes. As indicated by the name of this class, the adult skeleton is made largely of bone, a feature characteristic also of all four-legged vertebrates. Bony fishes typically have scaly skin, paired fins, and gills covered by a hinged bony plate, the operculum, on each side of the pharynx. The animals also develop an internal membranous sac, pouched out ventrally from the

pharynx. In most species this sac becomes a swim bladder. In so-called lungfishes, however, the sac functions partly like a lung.

Amphibia. The two main groups of this class are, first, the salamanders and newts, in which a tail is present throughout life, and second, the frogs and toads, which are tail-less as adults. Frogs and toads may be distinguished by their dentition: frogs possess teeth on their upper jaws, toads do not. All amphibia have smooth, moist, glandular skins without scales and two pairs of legs. Tadpole larvae typically live in fresh water, are fishlike in most respects, and breathe by means of gills and through the skin. The adults of all newts, some salamanders, and some toads are aquatic, and the adults of all others are terrestrial. Virtually all adults have lungs, and the newts and some of the aquatic salamanders in addition retain the gills throughout life. The heart of amphibia is three-chambered: two auricles and one ventricle. In most species, fertilization and embryonic development take place in water, regardless of whether the adults are terrestrial or not.

Reptilia. Many people tend to confuse these true land vertebrates with amphibia. But reptiles are easily identified by their dry, scaly skin, by the presence of a fairly well defined neck, and by their large shelled eggs, which are always laid on land, even where the adults are aquatic (Table 6). The living representatives of this class are mainly turtles and tortoises, snakes and lizards, and alligators and crocodiles. The legs of reptiles are typically five-toed and equipped with claws. But in sea turtles they are modified into flippers, and in snakes and some lizards limbs are not present at all. Gills are nonfunctional embryonic structures, and breathing is always by lung. This, and a four-chambered heart, are characteristic also of birds and mammals. Reptiles, birds, and mammals are alike also in that fertilization occurs within the body of the female, not in open water.

Aves. In their internal structure, these feathered vertebrates greatly resemble primitive reptiles. Apart from the presence of feathers, birds are characterized by forelimbs, which are modified into

wings, and by the absence of teeth, the mouth armature being a horn-covered beak or bill. Birds maintain a constant body temperature, like mammals. Undoubtedly because of the aerodynamic requirements of flight, birds are more like one another than the members of any other vertebrate class. We may note, however, that many birds have reduced wings and cannot fly. Ostriches, emus, moas, kiwis,





FIG. 9.37. Egg-laying mammals, or Prototheria. (a) A spiny anteater. (b) A duck-billed platypus. (American Museum of Natural History.)

and penguins are among the flightless types. Of the 10,000 or so avian species, more than half belong to a single order, the passerine, or perching, birds, which include most of the familiar bird types.

Mammalia. The female members of this class possess milk-producing mammary glands, and they nurse their young. Three other identifying features are the possession of hairy skin, the transverse division of the body cavity by a diaphragm, and the nonnucleated condition of mature red blood corpuscles. The class comprises some 6,000 species, grouped into three subclasses. The subclass Prototheria consists of egg-laying types. These are the least progressive mammals, and they still display many ancestral reptilian features. The group today

includes only the duck-billed platypus and the spiny anteaters (Fig. 9.37). Pouched or marsupial mammals form the subclass Metatheria. In these, the young are born in a very incompletely developed state, and development is completed in an abdominal skin pouch of the female. Opossums and the kangaroos, koala bears, wombats, and other marsupials of Australia belong to this group. The vast majority of mammals are included in the subclass Eutheria, the placental mammals, in which the young develop within the uterus of the female. Among these most familiar of all living organisms, shrews are the tiniest, whales the largest, and rodents the most numerous. The primates, which include man, are the brainiest mammals.

REVIEW QUESTIONS

- 1. What structural and functional features distinguish most animals from most plants? What are the chief nutritional patterns among animals? How does alimentation influence the general structural and functional organization of animals?
- 2. How does the requirement of locomotion influence the general architecture of an animal? Contrast the basic design of moving and nonmoving animals.
- 3. Which phyla are included among the Radiata, and what diagnostic features distinguish these phyla?
- 4. Which are the pseudocoelomate phyla, and what features characterize the group as a whole? Describe the structure and the life cycle of rotifers. Which are the schizocoelomate phyla?
- 5. What is the fundamental body plan of mollusks? Describe the internal structure of animals within each of the molluscan classes.

- 6. Describe the diagnostic features of annelids. Name the annelid classes.
- 7. Describe the group characters and the basic body organization of arthropods. Name the classes and the distinguishing features of each. Show how segmentation is exploited adaptively in (a) crustacea, (b) insects.
- 8. Which phyla are included among the enterocoelomates, and for what reasons? How do these phyla differ from one another? State the group characteristics of echinoderms, and name the various classes. Describe the structure of a starfish.
- 9. Review the classification of chordates. Contrast the diagnostic features of the subphyla.
- 10. Describe the group characteristics of vertebrates. Name the classes, and describe the identifying features of each. Which classes are (a) tetrapods, (b) jawless, (c) warm-blooded, (d) gill breathers, (e) lung breathers?

SUGGESTED COLLATERAL READINGS

Buchsbaum, R.: "Animals without Backbones," University of Chicago Press, 1948.

Griffin, D. R.: The Navigation of Bats, Sci. American, vol. 183, 1950.

Lyman, C. P., and P. O. Chatfield: Hibernation, Sci. American, vol. 183, 1950.

McLean, F. C.: Bone, Sci. American, vol. 192, 1955.

Milne, L. J., and M. J. Milne: Temperature and Life, Sci. American, vol. 180, 1949.

Rodbard, S.: Warmbloodedness, Sci. Monthly, vol. 77,

Romer, A. S.: "Man and the Vertebrates," University of Chicago Press, 1941.

Storer, J. H.: Bird Aerodynamics, Sci. American, vol. 186, 1952.

Part Three METABOLISM

Up to this point, our primary concern has been the "what" of living matter: What is the character of the living world as a whole? What are the structures and functions of the living substance, and what kinds of living organisms exist on earth? In the remainder of this book, we shall continue to heed the what, but our primary concern will be the "how": How does the living world come into being, and how is it maintained? How are the

structures developed, and how are the functions carried out? In other words, our preoccupation will be less with the organizational than with the operational nature of living matter.

The operations of protoplasm are circumscribed by two words: metabolism and self-perpetuation. In this sequence of chapters, we deal with the first. Metabolism, we recall, may be described roughly as a group of processes which makes the living machinery run, which transforms an otherwise inert system into an active one. Specifically, metabolism includes, first, **nutrition**; second, the production of internal energy, or **respiration**, made possible by some of the nutrients; and third, the **utilization** of raw materials and of energy, always toward chemical activities such as synthesis of new protoplasmic components, sometimes toward physical activities such as movement (Fig. 10.1).

Nutrition is auxiliary to the remainder of metabolism. This remainder occurs within individual cells and thus constitutes **cellular metabolism**. It is the main phase of all metabolism, for only if its cellular motors are running can the whole organism be alive.

CHAPTER 10

Autotrophic nutrition

Every organism must supply itself in some way with various inorganic and various organic nutrients. According to how the nutrients are obtained, an organism is either an autotroph or a heterotroph.

An autotroph requires from its environment inorganic nutrients *only*. From some of these, it then manufactures, by its own efforts, all necessary organic nutrients. By contrast, a heterotroph is unable to create organic substances out of inorganic ones. Therefore, it requires from its environment not only inorganic nutrients, but also certain kinds and quantities of prefabricated organic nutrients.

Evidently, since organic nutrients, or *foods*, can be created only by autotrophs, heterotrophs ultimately depend on autotrophs for their organic supplies.

AUTOTROPHIC PATTERNS

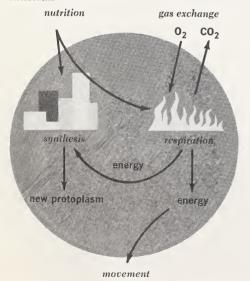
Inasmuch as the essential problem of autotrophs is to manufacture organic nutrients, and inasmuch as organic substances are identified by the presence of *linked* carbon atoms, we may say that the essential problem of autotrophs is to combine a number of single-carbon molecules into larger molecules containing linked carbons. In all autotrophs, the

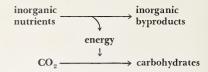
single-carbon molecules serving as raw materials are molecules of CO₂. And the larger molecules produced, each containing linked carbons, are carbohydrates. These carbohydrate foods may later be transformed into all other organic materials needed in protoplasm.

The conversion of CO₂ into carbohydrates involves *synthesis* reactions, hence energy. Two kinds of autotrophs may be distinguished according to the energy sources they employ: **chemosynthesizers** and **photosynthesizers**.

As noted in Chap. 2, chemosynthesizers are found among bacteria and the energy sources are various inorganic substances. These substances are absorbed by bacteria as nutrients from the environment, and within a bacterial cell the nutrients then undergo certain chemical reactions which yield energy. This energy is used subsequently to convert CO₂ into carbohydrates. The general pattern is (see also Fig. 2.9)

FIG. 10.1. The main component processes and results of metabolism.





Among specific inorganic nutrients used by various chemosynthetic bacteria are hydrogen, sulfur, iron, and nitrogen compounds. Accordingly, these bacteria are named hydrogen bacteria, sulfur bacteria, iron bacteria, and nitrifying and denitrifying bacteria. We have discussed the activities of the last two in connection with the global nitrogen cycle (Chap. 5).

Far more abundant, and far more important generally, are the photosynthetic autotrophs. As we already know, they are found abundantly among the Monera and Protista, and the Metaphyta consist entirely of photosynthesizers. Their energy source for food manufacture is light, and *chlorophyll* is the agent which traps light energy and makes it available for food production. The general pattern is (see also Fig. 2.10)

$$\begin{array}{c} \text{light} & \longrightarrow \text{chlorophyll} \\ & \downarrow \\ \text{energy} \\ & \downarrow \\ \text{CO}_2 & \longrightarrow \text{carbohydrates} \end{array}$$

The product of photosynthesis, i.e., carbohydrate, consists of carbon, oxygen, and hydrogen. It is clear, therefore, that CO₂ cannot be the only raw material required for carbohydrate manufacture. A hydrogen source is needed also, and that source is water. In addition to CO₂ and water, photosynthetic autotrophs require a great many other inorganic nutrients as well. For example, a usable nitrogen source is needed for protein production; a magnesium source is needed for chlorophyll production. In general, wherever a protoplasmic material contains a mineral component, that component must be obtained from the environment.

Thus the overall pattern of autotrophic nutrition may be considered to consist of three broad groups of processes:

- 1. Procurement of inorganic nutrients from the environment, including CO₂, H₂O, and a variety of other mineral substances
- 2. Internal transportation, of both inorganic raw materials and finished organic products, to all parts of the organism
- 3. Manufacture of organic nutrients, i.e., photosynthesis, out of some of the inorganic raw materials

We shall discuss each of these processes as they occur in tracheophytes specifically.

THE INORGANIC NUTRIENTS

The raw materials needed by a land plant are obtained from two sources, air and soil. Air contributes most of the CO₂; soil contributes most of the water and other mineral substances. As noted in Chap. 8, green cells in leaves are in direct contact with the external air. Stomata and the interconnected air spaces in the mesophyll permit free circulation of air through a leaf. Carbon dioxide (and also oxygen and water vapor) may therefore be absorbed directly by each leaf cell, right where the gas will eventually be used in photosynthesis. On the other hand, liquid water and minerals cannot be absorbed directly by green cells, for these materials are present only in soil.

Soil

Soil consists principally of two components. One is sand, i.e., tiny eroded particles of rock. Such rock fragments generally have rough, jagged texture, and when they pack together they still leave small air spaces between them. Extremely small rock particles may pack together very tightly, leaving hardly any air spaces. This kind of sand is called *clay*. The other component of soil is humus. It consists of complex organic materials produced by the decay of previously present living matter. Humus to some extent binds the sand particles together and gives soil its crumbly, water-retaining character.

Actually, soil is not an essential medium for

photosynthetic organisms. For example, floating aquatic green organisms do very well without it. Moreover, land plants too can be maintained adequately if their roots are simply immersed in mineral-rich water, called hydroponic cultures. Evidently, so long as the environment provides water and minerals at all, it does not matter too much through what medium the plant obtains these materials. On land, soil happens to be the usual and the cheapest, hence the most treasured, large-scale supplier. And it has the additional very essential property of anchoring plants mechanically, without halting the continuous expansion of root systems.

General references to "soil" are usually references to the topsoil, the upper, most valuable layer. Topsoils differ widely in color, according to the types of minerals and humus materials contained in them. From the standpoint of plant nutrition, black soils generally are the richest. The roots of small plants are embedded entirely in topsoil. Larger plants send their roots into the extensive subjacent layer, the subsoil. Here the proportion of clay is high; hence subsoil is relatively dense and humus is virtually absent. Subsoil is usually underlain by loose rock, and this layer extends down to the continuous bedrock of the continent (Fig. 10.2).

The quality of topsoil depends on a wide variety of factors. A good topsoil is neither too dense to prevent the growth of roots nor too loose to be blown away or washed away. Also, a good soil contains a high proportion of water-retaining humus and is underlain by a substantial layer of subsoil, which prevents water from draining away too fast (Fig. 10.3).

Soil water holds various minerals in solution. Such soil minerals are present largely in the form of ions, and they get into soil water in three ways. First, most importantly, through *chemical dissolution* of the sand particles of soil by water and weathering. Second, through the *decay* of dead organisms, which returns to soil the minerals removed by living matter and which also adds to the humus content of soil. And third, through *nitrogen*

200



FIG. 10.2. Profile of soil. Note dark topsoil, underlain by light-colored layer of subsoil. Streaked layers of clay lie under the subsoil, and clay merges into rock near the bottom of the photo. (U. S. Department of Agriculture.)

FIG. 10.3. Aerial view of contour-plowed region. In contour plowing, plow lines are run at right angles to the slope of the land to reduce wind and water erosion. (U. S. Soil Conservation Service)



fixation and nitrification by bacteria, which increases the nitrate (NO₃-) supply of soil (Chap. 5).

To prevent nutritional exhaustion of intensively cultivated land, man is often forced to augment these relatively slow natural processes of replenishment. He may do so by various procedures. For example, he may add mineral-rich fertilizers to soil. He may let soils rest for one or more seasons. He may grow crops and, instead of harvesting them, may plow them right back into the ground. Or he may adopt a program of crop rotation, whereby different crops are planted in successive seasons, each crop requiring different sets of soil minerals.

The kinds of mineral ions normally required by plants usually include, for example, nitrate (NO₃⁻), phosphate (PO₄⁼), carbonate (CO₃⁻), sulfate (SO₄⁻); and potassium (K⁺), calcium (Ca⁺⁺), magnesium (Mg⁺⁺), copper (Cu⁺⁺), and iron (Fe⁺⁺⁺).

Absorption

All parts of the root epidermis may absorb soil nutrients. Since some 90 per cent of the available root surface is provided by the root hairs (Chap. 8), most of the absorption occurs there. As noted earlier, root-hair zones advance continuously as the root grows. Therefore, by the time one region of soil is more or less depleted of raw materials, root-hair zones have already advanced to a new region.

A great deal of water absorption is accomplished through osmosis. Protoplasm within a root hair normally contains a higher concentration of dissolved particles than soil water. Osmotic pressure therefore pulls soil water into the root hair. However, a simple test shows that osmotic force cannot be the only agency responsible for water absorption. If the soil is made to contain a higher concentration of dissolved particles than root-hair protoplasm, for example, by putting salt into soil, then the plant should lose water to the soil. Yet under such conditions the roots still take up water, though less than before (Fig. 10.4). Clearly, osmotic pull normally contributes some absorptive force, but another agency contributes even more. What is that other agency? It is active absorptive work done by the

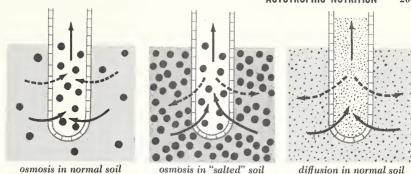


FIG. 10.4. Left: osmosis in roots. Particle concentrations are greater in root protoplasm than in soil; hence more water moves into root protoplasm from soil than in the reverse direction. Middle: the effect of "salting" the soil. Even if the particle concentration is made greater than in root protoplasm, water still moves into the roots (solid arrows), against the osmotic gradient (broken arrows). This indicates that osmosis is not the only agency in water absorption; active absorption in living root cells is of equal or greater importance. Right: diffusion in roots. Because root protoplasm contains a higher concentration of mineral ions than soil, ions should be expected to diffuse out of roots (broken arrows). Yet ions actually migrate from soil into roots (solid arrows), against the diffusion gradient. This indicates that diffusion cannot be responsible for ion absorption. Active absorption by living root cells is involved instead.

living root cell. Energy is required for this work. When the energy-liberating machinery of the cell is stopped with poison, then biological water absorption is stopped too, though osmotic, physical absorption still continues.

This "living" aspect of absorption is also illustrated clearly in the uptake of soil minerals. If the root-hair membrane were merely passive, like cellophane, then we should expect ions to diffuse from higher to lower concentrations; that is, ions should migrate from the more concentrated root protoplasm into the less concentrated soil water, until the concentrations on each side of the membrane were equal. In other words, root protoplasm should lose ions to the soil. This does not happen. On the contrary, ions migrate from the soil into the root, against the prevailing diffusion gradient (Fig. 10.4). Here again, energy- and oxygen-consuming work is done by the epidermal cells of the root. Their membranes are selective, moreover. Some ions are passed

through readily; others are not. Thus a plant absorbs soil nutrients in small part through purely physical processes and in large part through active, biological work performed by the root epidermis.

What happens to the water and the minerals absorbed into a root-hair cell? The most immediate effect is that the excess water tends to dilute the protoplasm of the cell. Should we not also expect that cell to swell up? We should indeed, but this does not happen to any appreciable extent. For most of the absorbed water and the dissolved materials are removed almost as soon as they enter the cell. The fluid is taken up by the cortex cells immediately adjacent to the root epidermis. This transfer essentially repeats the original process of water absorption. As epidermis cells tend to become more diluted by soil water, concentrations in these cells become lower than in adjacent cortex cells. The latter therefore pull water into them osmotically. Moreover, they also actively absorb water from the

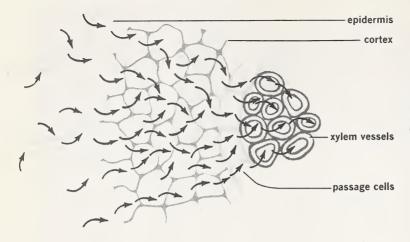


FIG. 10.5. The absorption path within a root. Water and dissolved minerals are absorbed by successively deeper layers of cells. Supplies so reach the xylem vessels near the root core.

epidermal layer. As a result, water which first had been in the soil, and then in the epidermis, is now in the outermost layer of the root cortex. *These* cells then tend to swell up, and their protoplasms tend to become more dilute. But water is now transferred again, into the next inner layer of cortex cells (Fig. 10.5).

In this manner, water and minerals are drawn progressively from cell layer to cell layer, toward the core of the root. Some of these nutritional supplies are retained by the cells along the route, but the bulk soon reaches the root endodermis. We recall the presence of unsuberized passage cells in this layer (Chap. 8). These provide a path into the root xylem. Water and dissolved materials are drawn into the passage cells, and from there they are pushed into xylem vessels.

Pushed is the right word. The water stream from soil xylem vessel is continuous and uninterrupted, and it is not a stream which trickles lazily by its own weight. Rather, the combined osmotic pressure and the combined absorptive pressure of all root cells are behind the water, and this root pressure drives water forcefully into the xylem tubes at the root core.

INTERNAL TRANSPORT

Once inorganic nutrients have been absorbed by the roots, they must be distributed to the rest of the plant. In particular, the green photosynthesizing tissues must be supplied. Further, after photosynthesis in leaves has produced foods, these must be distributed to all nongreen tissues which do not manufacture foods on their own. The traffic of inorganic nutrients from the roots upward occurs in the xylem, and the traffic of organic nutrients from the leaves downward, and also in the reverse direction, occurs in the phloem.

Xylem conduction

Xylem tubes are never empty of water. Even before a xylem vessel becomes functional, i.e., at a stage when only a column of newly formed xylem cells marks the location of a future conducting vessel, protoplasmic water already fills the interior of the cells. Later, when the protoplasm disintegrates, the water remains. As the plant grows in length, new cells are joined to the top of the xylem vessel. Each added cell also adds a corresponding cylinder of water to the column below. Water thus grows up,

as the plant grows up. No matter how high the plant, therefore, continuous, uninterrupted water columns range from every root-hair membrane, through root cortex and xylem vessels, to every leaf mesophyll membrane.

Upward "transportation" consequently becomes a matter of adding water at the bottom of such columns and withdrawing an equivalent amount from the top, minus the fraction which living tissues incorporate into their substance. As we have seen, root-hair absorption adds water at the bottom and generates root pressure. This is one force which pushes the water columns up.

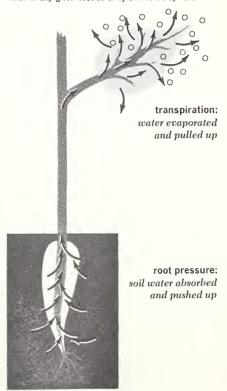
A second force, pull from above, is generated by transpiration, that is, evaporation of water from the leaves. As water vaporizes from a mesophyll cell, the cell tends to become partially dehydrated, and so the concentration of protoplasmic particles tends to increase. Osmotic pressure therefore draws water in from neighboring cells. These cells now tend to become partially dehydrated. Osmotic pull is propagated back in this manner, along cell paths leading to xylem terminals. This osmotic action of leaf cells pulls water up through the xylem, in quantities equivalent to the amount evaporated (Fig. 10.6). The effectiveness of this pull from above is familiar to everyone. An isolated leaf, or a flower with a stub of stem and a few leaves, survives for a considerable time when put into a glass of water: as water transpires from exposed plant tissues, fluid is pulled up from below.

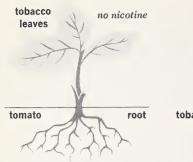
It should be clear that such a mechanism of transport depends on uninterrupted continuity of the water columns. The condition that the transport fluid is water, rather than another medium, greatly facilitates the maintenance of column continuity. For water possesses a high degree of *cohesion*. Individual molecules attract one another rather strongly, and a column of water therefore "hangs together" with appreciable tenacity. If the continuity of water in xylem vessels were broken by emptying them, then these vessels could never again function as water conductors. For neither the roots nor the leaves, nor both together, can raise a

whole new column of liquid from the ground to the leaves through air-filled vessels.

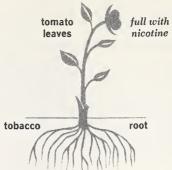
The key point in xylem transport is that the power source lies in living roots and leaves. The nonliving xylem tubes as such are passive, in the same way that a pipeline between two pumping stations is passive. Conduction through phloem is different in this respect. In this system the power source is spread out all along the transportation route.

FIG. 10.6. Xylem tubes contain continuous columns of water. Root pressure adds more water at the bottom, and transpiration removes water at the top through evaporation. Hence water in any given section of xylem moves upward.





graft shows nicotine is not formed in leaves but in roots of tobacco plant



graft shows nicotine transported upwards from tobacco root

FIG. 10.7. If tobacco leaves are grafted onto tomato roots (left), nicotine will be absent from the tobacco leaves. If tomato leaves are grafted onto tobacco roots (right), the tomato leaves will eventually contain nicotine. Experiments of this sort show that only tobacco roots manufacture nicotine and that this drug is transported upward by the phloem.

Phloem conduction

Unlike xylem, phloem is a two-way path. Downward conduction in phloem has long been known to occur: many roots store carbohydrates, which are photosynthesized only in leaf or stem. The occurrence of upward conduction has come to light through grafting experiments. For example, a stem of a tobacco plant grafted to a root of a tomato plant develops normal tobacco leaves, but these are entirely free of nicotine. Conversely, a tomato-plant stem transplanted to a tobacco-plant root produces tomato leaves, but these are full of nicotine. The first graft indicates that only the roots of a tobacco plant synthesize nicotine; the second graft, that the drug is transported upward. And since xylem channels are virtually free of nicotine, upward conduction must occur largely in phloem (Fig. 10.7).

Indeed, most of the organic nutrients of a plant travel in the phloem channel. Photosynthesized carbohydrates and their derivatives migrate from leaves and stem downward; organic storage products, and materials manufactured from them, travel from roots and stem upward. Some upward conduction of organic substances also occurs in xylem. For example, small amounts of sugar are generally present in this channel. In the case of the sugar

maple, this dilute xylem sap is processed into maple syrup.

We recall the composition of a phloem unit. A living companion cell is adjacent to, and presumably controls the functioning of, a section of sieve tube which contains cytoplasm but not a nucleus (Chap. 8). Transport through such units depends on diffusion. For example, mesophyll cells in the leaf photosynthesize, and so they acquire relatively high carbohydrate concentrations. Terminal phloem units in the vicinity do not photosynthesize; hence their carbohydrate content is lower. Consequently, diffusion tends to equalize the concentrations and the terminal phloem units absorb some of the mesophyll-produced carbohydrate. Their own carbohydrate content increases as a result, relative to that of lower phloem units next in line along the conduction path. These lower phloem units now absorb from units above them, and in this fashion nutrient conduction continues downward (Fig. 10.8). Cells along the way may retain greater or lesser amounts of the carbohydrate. But the bulk will be carried into the roots, step by step from one section of sieve tube to the next, under the impetus of the diffusion gradient pointing from the leaves toward the roots.

Alternatively, organic materials may be carried

upward, if the concentrations of such materials are high in the roots and lower above. This is the case, for example, in winter and early spring, when leaves are absent and photosynthesis does not take place. Organic nutrients stored in the roots during the preceding summer then travel upward into the food-requiring regions of the stem and the crown.

Phloem conduction, up or down, is slow compared with xylem conduction. In phloem, also, we do not find a distinct flowing sap, as in xylem vessels. The transportation medium, namely, sievetube protoplasm, flows and shifts within its cellulose confines only, but does not itself flow up or down bodily. Nutrient molecules alone are handed from one unit to the next. For this reason, nutrient conduction in phloem is often spoken of as translocation, a more specific designation than "transportation."

Xylem conduction to the leaves prepares the way for photosynthesis, and phloem conduction from the leaves distributes the results of photosynthesis. We are now ready to examine this third, and in many ways most crucial, component of autotrophic nutrition.

PHOTOSYNTHESIS

The fundamental importance of the set of reactions in which CO₂ and H₂O are transformed into carbohydrates cannot be overestimated. Carbohydrates produced through photosynthesis constitute the basic raw materials which, directly, or indirectly, give rise to all organic components of virtually all living matter and to virtually all living energy. The only organisms not dependent on photosynthesis are the chemosynthetic bacteria, which together amount to probably less than 0.01 per cent of all the protoplasm on earth.

The knowledge that CO₂ and water are among the raw materials, and carbohydrates among the products, makes it tempting to simply write, as a chemical "equation" for photosynthesis,

$$\mathbf{6H_2O} + \mathbf{6CO_2} \rightarrow \mathbf{C_6H_{12}O_6} + \mathbf{6O_2}$$

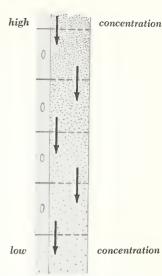


FIG. 10.8. The role of nutrient concentrations in phloem conduction. If a given nutrient is highly concentrated at one end of a phloem channel and less highly concentrated at the other, as shown, then a diffusion gradient will point from the high to the low concentration. The nutrient thus will be translocated in that direction.

This chemical statement, often regarded in earlier days as a correct representation of photosynthesis, is not only too simple, but also altogether incorrect. For in actual photosynthesis, CO₂ does *not* react with water. Such a reaction would produce simply carbonated water, never sugar! Moreover, sugar is not even the principal product of photosynthesis. Research in recent years has succeeded in elucidating the real chemical course of photosynthesis, and as we shall see, this course is quite different from what the equation above seems to suggest.

We may profitably begin a discussion of photosynthesis by inquiring into the role of chloroplasts.

Chloroplasts and chlorophyll

Chloroplasts are the cytoplasmic factories in which photosynthesis occurs. Into these bodies must come

all the raw materials, and light, and from them emerge the finished products.

A chloroplast is one of three kinds of plastids plant cells may possess. One kind of plastid does not contain any pigments. Plastids of this kind are found widely in roots and in the colorless tissues of stems and leaves. These bodies function primarily as *starch-storing* centers.

A second type of plastid contains so-called carotenoid pigments. These colored substances are of two kinds: the carotenes, which vary in color from cream white to turnip yellow, carrot orange, and tomato red; and the xanthophylls, which produce the bright yellows and browns of plants. In different plant species, carotenoid-containing plastids occur in roots, stems, leaves, flowers, fruits, or several of these plant parts together. Carotenoid pigments are widespread also among Protista (Chap. 7) and Metazoa (e.g., the yellow hue of egg yolk, butter, and other animal fats), and we may note that they are related chemically to vitamin A.

The third type of plastid contains both carotenoids and chlorophyll. Because chlorophyll is uniquely present in them, plastids of this kind are called chloroplasts. Only they are green, and only they function in photosynthesis.

The electron microscope shows that a chloroplast is composed of numerous grana (Fig. 10.9). These small granular bodies are the functional units in photosynthesis and the real "factories" for food production. Each granum consists of a series of protein layers, arranged like coins in a stack. Between



FIG. 10.9. Electron micrograph of a single chloroplast, showing the grana. (R. W. G. Wyckoff, "Electron Microscopy," Interscience Publishers, Inc., 1949.)

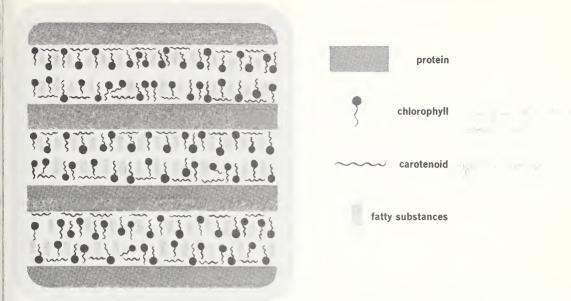


FIG. 10.10. Diagrammatic representation of the internal structure of a single granum of a chloroplast. Note the layered arrangement of the components.

every two such layers is a double layer consisting of fatty material, chlorophyll, and carotenoid molecules (Fig. 10.10). The fairly orderly arrangement of these molecules in the diagram may depict actual conditions. For the pigment molecules are believed to be positioned with a regularity approaching that of a crystal.

Blue-green algae do not possess chloroplasts. But they do contain individual grana, dispersed throughout the cell. Photosynthetic bacteria contain neither chloroplasts nor grana. The structure of the chlorophyll carriers in these organisms is still obscure.

In chloroplasts, the green pigment largely hides the red-yellow colors of the carotenoids present. Different plant types contain different proportions of these pigments; hence the various lighter and deeper shades of green in a landscape. In the fall, when the chlorophyll of the leaves disintegrates, the more stable carotenoid pigments become unmasked. These are mainly responsible for the brilliant autumn colors of plants. Many plants at that season also manufacture anthocyanin pigments, substances which are not within plastids but are free in cellular cytoplasm. The anthocyanins produce the deep reds, purples, and blues of plants. Some species contain anthocyanins throughout the year, in various body parts (e.g., the deep red of beet roots).

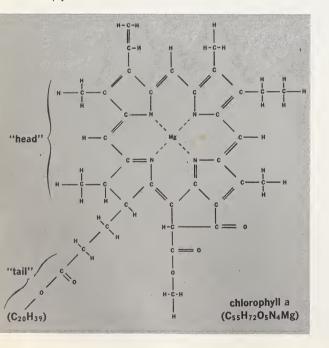
A green cell may possess from a few up to about 80 chloroplasts. In a mature tree, all the chloroplasts together may provide a surface area for light absorption totaling some 150 square miles. Chloroplasts reproduce within cells. Thus the chloroplast population of a cell may keep pace with the multiplication of the cell itself.

Chlorophyll is the all-important pigment in a chloroplast. We already know that the variety

known as chlorophyll *a* is of particular significance (Chap. 7). It is present in a photosynthetic organism regardless of what other chlorophyll varieties may also be present, and we shall find, indeed, that chlorophyll *a* plays a special role. Chlorophyll molecules consist, essentially, of four complex carbonnitrogen rings, which in turn are combined into a larger ring, the "head" of the molecule. At the center of this head is a single atom of magnesium, held to the smaller rings by side linkages. A "tail" of linked carbons is attached to one of the smaller rings (Fig. 10.11).

It is interesting to note that this structural pattern of chlorophyll is remarkably similar to that of heme, the colored component of hemoglobin in animal blood cells. An atom of iron is in the center

FIG. 10.11. The chemical structure of a molecule of chlorophyll.



of heme, in place of magnesium, and some other differences exist. But in major structural respects, the most important plant pigment and the most important animal pigment are intriguingly alike.

Light and water

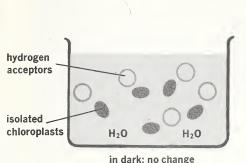
What happens when light enters a chloroplast and strikes a chlorophyll molecule? The important event is that the molecule absorbs a portion of the light energy. As is well known, visible sunlight consists of a series of light waves, each producing a characteristic "rainbow" color—red, orange, yellow, green, blue, or violet. Each of these light waves contains energy; red waves have the least energy, violet waves the most. When a mixture of these waves, as in sunlight, falls on a chlorophyll molecule, the molecule absorbs much of the red, orange, and yellow waves and much of the blue and violet waves. It is so constructed that it does not absorb the green waves but lets these go right on without change. That is why, when we look at a leaf illuminated by sunlight, it appears green to us. The chlorophyll in the leaf has absorbed all but the green waves in sunlight.

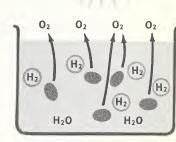
Because it absorbs certain light waves, chlorophyll also absorbs a certain amount of energy. We say that chlorophyll becomes excited; that is, it contains more energy after illumination than before.

Several years ago, an ingenious experiment showed what excited chlorophyll does with its absorbed solar energy. Leaves were dried and powdered, and the chloroplasts in this powder were isolated and cleaned. The pure chloroplast preparation was then suspended in water to which certain iron salts had been added, and the whole was illuminated. The result: as soon and as long as the light was on, the chloroplasts actively evolved bubbles of oxygen (Fig. 10.12).

Since such an experiment does not involve living cells, carbohydrate production cannot be expected to occur, and indeed it does not occur. But the experiment does involve light, chloroplasts, and water, and this combination evidently remains functioning. The formation of oxygen bubbles must

FIG. 10.12. The functions of light and chlorophyll. Chloroplasts and hydrogen acceptors are suspended in water. In the dark, no change occurs (left). If the light is turned on, oxygen bubbles form (right). This indicates that water is split in the chloroplasts with the aid of light energy. Free oxygen escapes, and the hydrogen of split water is picked up by the hydrogen acceptors.





in light: oxygen bubbles out

mean that water is *split* into hydrogen and oxygen, for the only source of the oxygen here could be the water present. Further, light energy, via chlorophyll, must do the splitting, for the experiment does not work without either light or chlorophyll. The added iron salts serve merely as acceptors, or absorbers, of the hydrogen of split water. We may conclude that the function of light in photosynthesis is to supply the energy required for the splitting of water and that the function of chlorophyll is to trap this energy and so to make the splitting possible.

In other words, splitting up water into hydrogen and oxygen turns out to be *the* important role of light and chlorophyll. Chlorophyll evidently functions as an energy carrier. Excited chlorophyll, carrying light energy, releases this energy, which then splits water. The chlorophyll at this point is no longer excited, but it may be illuminated again, and it may then trap more light energy for more water splitting.

We may note here that *only* chlorophyll *a* can directly split water. After being illuminated, other varieties of chlorophyll may transfer their trapped energy to chlorophyll *a* and so may help indirectly in splitting water. But the actual splitting requires energy delivered by chlorophyll *a*. After water is split, the liberated oxygen becomes an escaping by-

product and does not contribute further to photosynthesis. This leaves the liberated hydrogen; it must be the element which then reacts with CO₂, yielding carbohydrate. That this is actually so is now well established.

Thus photosynthesis as a whole may be envisaged as a two-step process. The first step may be called photolysis ("light splitting"). It involves, as just discussed, the cleaving of water molecules into separate hydrogen and oxygen, with the aid of light energy trapped by chlorophyll. The second step may be called \mathbf{CO}_2 fixation. It involves the combining of \mathbf{CO}_2 with hydrogen, resulting in the formation of carbohydrate. These two steps may be symbolized diagrammatically as in Fig. 10.13.

In the next section we shall examine some of the details of CO₂ fixation.

CO₂ fixation

The combining of CO₂ and H₂ is not a simple, single reaction. Rather, CO₂ fixation is now known to occur through a *cycle* of many reactions. Such a cycle operates somewhat like an endless belt of an assembly line in a factory. As such a belt moves along, a steady stream of raw materials is funneled to it at one point and these materials are processed by various workers or machines along the way. A

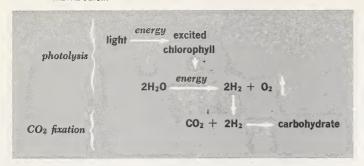
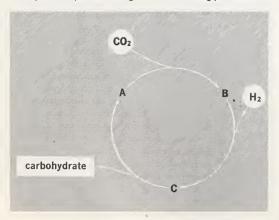


FIG. 10.13. The general pattern of the two phases of photosynthesis, i.e., photolysis and CO₂ fixation. Both phases take place within the grana of chloroplasts.

stream of finished products then emerges at another point, and the empty portions of the belt return to the starting point, where they pick up new batches of raw materials. Many vital metabolic transformations, in plants as well as animals, are known to occur through such cyclical sequences.

The particular cycle of CO_2 fixation may be generalized as in Fig. 10.14. Note here that A, B, and C in the diagram are specific molecules known to be present in chloroplasts. These molecules may be

FIG. 10.14. The general pattern of the CO₂-fixing cycle. In segments AB, CO₂ enters as raw material, and in segment BC, hydrogen enters as raw material. Segment CA yields the carbohydrate endproduct and regenerates the starting point A.



regarded as the "endless belt." In the cycle segment AB, which consists of many reactions, CO_2 enters as a raw material. In the segment BC, which again consists of many reactions, H_2 obtained through photolysis enters as a second raw material. And the segment CA, similarly including many reactions, yields the final carbohydrate product, and it also "regenerates" the starting condition.

It can be shown that this CO₂-fixing cycle must "go around" three times before one molecule of finished carbohydrate is obtained. In other words, three CO₂ molecules must enter the cycle, one molecule in each turn. In these three turns, 6H₂ are used up, obtained from the earlier photolysis of 6H₂O (which has produced 6 O, or 3 O₂, as byproduct). The yield of three turns of the cycle, then, is one molecule of finished carbohydrate. Three molecules of water form as net byproduct also. We may summarize these requirements and yields as in Fig. 10.15.

Note that water is both a raw material and a byproduct: six molecules are used up, but three molecules reappear later. Note also that the one resulting carbohydrate molecule is *organic* and that it contains three linked carbon atoms: the three *single* carbon atoms which enter the cycle in the form of inorganic CO₂ emerge as three *linked* carbon atoms in the form of organic carbohydrate. The whole function of photosynthesis is to produce this three-carbon molecule with linked carbons. What actually is this endproduct, and what happens to it?

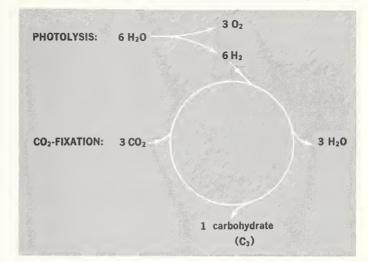


FIG. 10.15. The unit process in photosynthesis. An input of $6\mathrm{H}_2\mathrm{O}$ and $3\mathrm{CO}_2$ yields, through photolysis and CO_2 fixation, an output of $3\mathrm{O}_2$, $3\mathrm{H}_2\mathrm{O}$ and one molecule of carbohydrate. The latter, in its C_3 skeleton, joins the three single carbons put in as CO_2 .

The endproduct

The name of the carbohydrate product of photosynthesis is **phosphoglyceraldehyde**. It may be called **PGAL** for short, and its atomic formula is $C_3H_5O_3$ — \mathbb{P} , where — \mathbb{P} is a *phosphate* group. In this C_3 compound, the three carbon atoms are linked into a chain. **PGAL** is a *food*. A plant nourished artificially with prefabricated **PGAL** may survive, without photosynthesis and without any other organic supplies.

As PGAL forms in the grana, it does not accumulate to any great extent. For it rapidly undergoes one of three main fates: it may be used right away as a *nutrient* in the cell which produced it; it may be "packaged" for *export* to other cells; or it may be packaged for *storage*.

Phosphoglyceraldehyde is usable immediately as a respiratory fuel. It may happen, therefore, that some of the PGAL just manufactured is burned at once to provide the energy for more CO₂ fixation. PGAL is also usable directly as a building material, and it may contribute to the construction of any of the innumerable protoplasmic components of

plant cells. For example, PGAL just produced could be used to build anew, or to repair, some of the chemical machinery required for PGAL production itself.

But a green cell generally manufactures much more PGAL than it requires for its own maintenance. The bulk of the photosynthetic product becomes available for export through the phloem to root cells, stem cells, and nonphotosynthesizing cells in general. However, PGAL is not exported as such. It is probably too reactive a material. In transit from leaf to root, for example, it would react with other substances long before it could reach its destination. A less reactive, "packaged" form of PGAL would clearly be more advantageous. The green cell actually does package PGAL, by converting it to glucose.

In this conversion, two molecules of PGAL are combined into one molecule of glucose. This occurs through a lengthy series of reactions in which the two PGAL molecules are joined, their phosphate groups are removed, and hydrogen atoms are substituted for them. The reaction sequence is of considerable importance in respiratory metabolism

as well, and we shall deal with it again in that context. Here a general summary will suffice:

$$\begin{array}{c} 2 \; C_{\scriptscriptstyle 3} H_{\scriptscriptstyle 5} O_{\scriptscriptstyle 3} - \raisebox{-3pt}{$\stackrel{\textstyle \sim}{\tiny}$} \xrightarrow{} C_{\scriptscriptstyle 6} H_{\scriptscriptstyle 12} O_{\scriptscriptstyle 6} \\ \\ PGAL & glucose \end{array}$$

We may note generally, for animals as well as plants, that if carbohydrates are to be transported from cell to cell or from tissue to tissue, the vehicle is primarily glucose. This sugar is less reactive than PGAL, hence is not so likely to be altered chemically during transit. Since conversion to glucose and export to other cells is the fate of much of the photosynthesized carbohydrate, glucose is often, though not quite correctly, regarded as the primary endproduct of photosynthesis. Clearly, the green cells of a plant must in daytime manufacture enough PGAL for themselves and must export enough glucose to all other cells to suffice for a 24-hr period.

Actually, green cells normally produce enough PGAL to serve not only for current uses in all plant cells, but also to allow some of it to be stored.

Storage occurs largely in roots and stem, but leaves too generally store small amounts. Like carbohydrate transport, carbohydrate storage does not involve PGAL as such. In any storage problem, two considerations are paramount. First, the stored material should take up as little space as possible, and second, it should be "out of circulation," that is, relatively unavailable for continuous activities. Since PGAL reacts readily with protoplasmic components in its vicinity, it would not remain out of circulation for long. Even glucose, though less reactive, would enter metabolic processes fairly rapidly. Moreover, both of these carbohydrates take up considerable molecular space.

Plants have developed ways to "condense" PGAL molecules into more compact, sufficiently unreactive packets. This may take the form of dehydration synthesis, i.e., the joining together of two or more molecules, accompanied by a simultaneous removal of water. For example, the green cell may first produce glucose from PGAL as above. Two glucose molecules may then be joined, and one water molecule is removed at the same time:

$$C_6H_{12}O_6 + C_6H_{12}O_6 \rightarrow C_{12}H_{22}O_{11} + H_2O$$

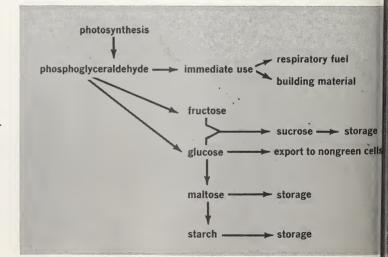


FIG. 10.16. The possible fates of PGAL.

The resulting 12-carbon carbohydrate is maltose, malt sugar, a disaccharide (Chap. 6). Maltose may now be stored as such, or pairs of maltose molecules may be combined and condensed further, until some two dozen glucose units have been joined into a single very large molecule:

$$24C_6H_{12}O_6 \rightarrow C_{144}H_{240}O_{120} + 24H_2O$$

This very large molecule is starch. It is smaller by 24 water molecules than 24 individual glucose molecules, and it is very much less reactive. Hence it is eminently suitable as a storage form of carbohydrates and it is actually very common among plants. Starches vary somewhat in composition; that is, they may contain more or fewer than 24 glucose units per molecule. The generalized formula for starch may be written $(C_6H_{10}O_5)n$, where n is the number of glucose units per molecule.

Maltose and starch are not the only storage forms of the photosynthetic product. Some plants build PGAL into storage fats (e.g., olive oil, castor oil). Others make a variety of storage sugars. For example, PGAL may be converted partly into glucose, partly into fructose. Glucose and fructose may then be combined pairwise into sucrose, a disaccharide:

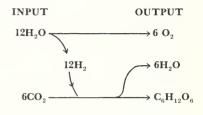
$$\begin{aligned} \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 + \mathbf{C}_6\mathbf{H}_{12}\mathbf{O}_6 &\to \mathbf{C}_{12}\mathbf{H}_{22}\mathbf{O}_{11} + \mathbf{H}_2\mathbf{O} \\ \text{glucose} & \text{fructose} & \text{sucrose} \end{aligned}$$

Sugar cane, sugar beets, as well as many kinds of fruits owe their sweetness to stored fructose and sucrose.

Storage syntheses of this sort occur both in green and in nongreen cells. In the latter, imported glucose is the starting material and nonpigmented plastids often are the sites of storage, as noted earlier in this chapter.

Whenever one of these cells must draw on its stored reserves, the exact reverse of storage synthesis takes place. For example, starch may be converted into glucose by chemical *addition* of water. The various possible fates of the photosynthetic end-product are indicated in Fig. 10.16.

The pattern of photosynthesis as a whole is outlined in Fig. 10.17. Since two PGAL molecules are required for the manufacture of one glucose molecule, the CO₂-fixing cycle must go around six times before one glucose molecule can be obtained. The requirements and yields under such conditions then are:



or

Note here that input and output balance. And note also that the last chemical statement is *not* a real equation; as we have seen, CO₂ actually reacts with H₂, not with H₂O.

Inorganic nutrients, plus foods in the form of PGAL or its derivatives, now are available to each plant cell. Autotrophic nutrition is completed at this point, and it becomes the task of the individual plant cell to utilize these nutrients in cellular metabolism, i.e., respiration and synthesis. Before we examine these processes, we inquire into the equivalent nutritional events encountered among heterotrophs.

REVIEW QUESTIONS

1. Define metabolism. What major processes are included under this term? Define nutrition. Define autotrophic nutrition. Review the various autotrophic pat-

terns of life. How does chemosynthesis differ from photosynthesis?

2. What are the components of topsoil? What layers

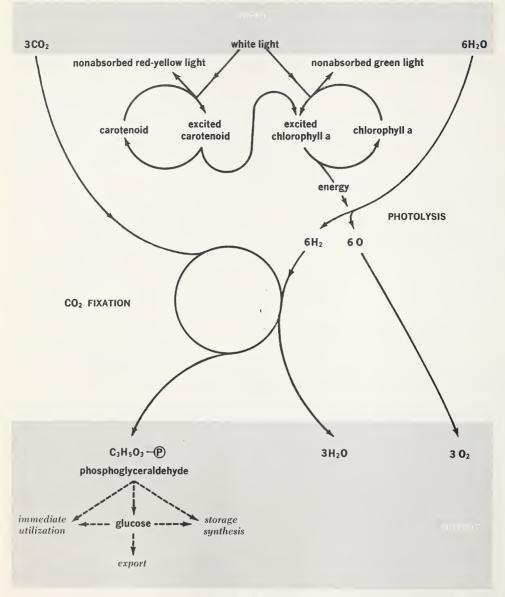


FIG. 10.17. Overall summary of photosynthesis.

are found under the topsoil? In what ways do plants depend on soil? Review the ways in which soil minerals are replenished.

- 3. What are hydroponics, and how do they contribute to our knowledge of the nutritional requirements of plants? What are the specific kinds of inorganic raw materials a plant must obtain? Where, and through what processes, does a plant absorb (a) water and (b) other minerals?
- 4. How does a plant obtain atmospheric gases? Review the anatomical pathways by which a plant acquires and transports all the various categories of needed nutrients.
- 5. What is root pressure, and how is it generated? What is transpiration, and what role does it play in xylem conduction? What kinds of nutrients are transported in xylem, and in which direction?
- 6. What forces bring about phloem conduction? What kinds of nutrients are carried in phloem, and in which direction? Describe in detail the processes which would bring about the upward translocation of a given nutrient.
- 7. What are plastids, and what kinds are there? What is the internal architecture of chloroplasts? What major

- classes of pigments are usually found in plants? Where do these pigments occur, and what colors do they produce? What pigments are responsible for the colors of autumn leaves?
- 8. State the general chemical nature and function of photosynthesis as a whole. Review the sources of the carbon, the hydrogen, and the oxygen atoms which compose photosynthesized carbohydrates. What experiments have demonstrated the derivation of the oxygen in such carbohydrates?
- 9. What is the function of light and chlorophyll in photosynthesis? What experiments have demonstrated these functions? What are the events in photolysis and CO₂ fixation? Review the steps in each case.
- 10. What is the principal net endproduct of photosynthesis as a whole? Review the possible fates of this endproduct. What are the main transportation and storage forms of carbohydrates in plants, and how is the photosynthetic endproduct converted into these?
- 11. Review the detailed reaction sequences of all photosynthesis. What are the net input and the net output of the whole process? Review once more the place of photosynthesis in plant nutrition generally.

SUGGESTED COLLATERAL READINGS

- Arnon, D. I.: The Chloroplast as a Complete Photosynthetic Unit, Science, vol. 122, 1955.
- Aronoff, S.: Chlorophyll, Botan. Rev., vol. 16, 1950.
- Evans, R. M.: Seeing Light and Color, Sci. American, vol. 181, 1949.
- Frank, S.: Carotenoids, Sci. American, vol. 194, 1956.
- Greulach, V. A.: The Rise of Water in Plants, Sci. American, vol. 187, 1952.
- Kellogg, C. E.: Soil, Sci. American, vol. 183, 1950.
- Swanson, C. L. W.: Soil Conditioners, Sci. American, vol. 189, 1953.
- Thimann, K. V.: Autumn Colors, Sci. American, vol. 183, 1950.

CHAPTER 11

Heterotrophic nutrition

We recall that heterotrophs require inorganic as well as prefabricated organic nutrients from their environment. We also recall that heterotrophs are of three general kinds: saprophytes (e.g., certain bacteria and fungi), which absorb nutrient molecules, inorganic as well as organic, from dead or decaying protoplasm; symbionts (e.g., other bacteria and fungi and certain animals), which obtain their nutrient from given host organisms; and freeliving bulk feeders (e.g., other animals), which eat living or dead protoplasm. The nutritional processes of the latter, especially as they occur in man, will largely occupy us in this chapter.

HETEROTROPHIC PATTERNS

We have found in the preceding chapter that a plant cell may survive if it is given water and minerals and if it is supplied with, or is allowed to photosynthesize, organic carbon. From these three categories of nutrients, a plant cell is able to construct all the other components of its protoplasm. But if an animal cell is given only these three types of nutrients, it soon dies. For it requires three additional types of nutrients which, unlike the plant cell, it cannot manufacture on its own.

First, water, minerals, and photosynthesized organic carbon do not provide —NH₂, the important amino group present in all proteins and nucleoproteins. Plants are able to make —NH₂ out of mineral nitrates (Chap. 5). But animals cannot, and their cells therefore must be supplied with prefabricated —NH₂. Plants, or other animals which have eaten plants, must be the source of supply.

Second, plants can convert phosphoglyceraldehyde (PGAL), or glucose, or other forms of organic carbon, into all the vitamins they require. Animals cannot do likewise. Most animals do manufacture at least some of the vitamins, although, in many cases, only in inadequate quantities. Specific abilities here vary with the species, but no species is as self-sufficient in this regard as a green plant. Missing vitamins consequently must be supplied in prefabricated form, and plants are again the ultimate source of supply.

Third, unlike plants, animals are unable to convert organic carbon into all 23 kinds of amino acids needed for protein manufacture (Chap. 14). Depending on the species, 8 or 10 kinds, so-called "essential" amino acids, must be supplied prefabricated, and plants are the ultimate suppliers here too.

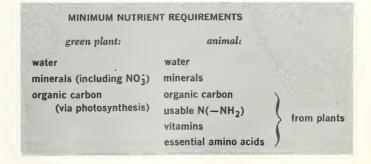
The minimum nutrient supplies to an animal cell therefore must include at least six types of materials: water, minerals, organic carbon, usable nitrogen, vitamins, and essential amino acids. Evidently, animals cannot survive without plants, which provide four of these six items (Fig. 11.1).

If an animal could obtain all the nutrients it requires in the form of pure, immediately usable molecules, it would not need an alimentary system. It could then simply absorb such molecules from the environment, through its cell surfaces. This is actually the nutritional pattern in several types of heterotrophs, e.g., saprophytes and many parasites. But apart from water and the minerals dissolved in water, directly usable nutrient molecules are largely unavailable to free-living bulk feeders. What is available to such animals is plant or animal protoplasm in bulk, living or dead. And we may note that it is the principal function of an alimentary system, first, to provide such bulk foods through ingestion, and second, to separate bulk foods into individual nutrient molecules directly usable by cells.

This second function is accomplished by <u>digestion</u>. *Mechanical* digestion first subdivides materials into fine particles suspended in water, and *chemical* digestion then reduces these particles to molecular dimensions. In the process, usable molecules become separated out and more complex molecules are broken up into smaller, usable ones.

Digestion produces a food solution in which three groups of substances may be found. First, there are nutrient molecules which animal cells require but cannot manufacture on their own. These comprise water, minerals, and the four categories of plant-derived substances listed above. Second, there are nutrient molecules which *can* be

FIG. 11.1. A comparison of minimum nutrient requirements of plants and animals.



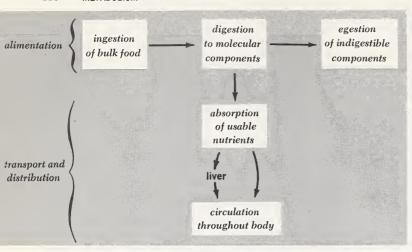


FIG. 11.2. The general pattern of animal nutrition

manufactured by animal cells but, since eaten food generally supplies them, need not be manufactured. For example, animal cells may manufacture fatty acids from organic carbon, but they may not need to do so if fatty acids are included in eaten food. And third, the food solution usually contains indigestible or otherwise unusable materials. Plant cellulose, for example, is a common indigestible component of bulk foods. Substances in this last category are eliminated, or egested.

But alimentation (i.e., ingestion, digestion, egestion) does not complete heterotrophic nutrition. For the usuable nutrients made available through alimentation must now be distributed to all cells of the organism. This involves, first, absorption of nutrients from the alimentary tract into the body circulation, and second, transport of nutrients by the circulation to all cells. Moreover, transport in many animals occurs indirectly via a liver, and the functioning of such an organ is of vital significance in nutrition. Finally, all these various processes in animals are controlled by nerves, by muscles, and in some also by hormones; hence these body components serve a nutritional role too.

We may diagram the general heterotrophic pat-

tern as in Fig. 11.2. We now proceed to examine each of the major phases.

INGESTION AND DIGESTION

Ingestion: hunger

What prompts us to eat what we eat? What makes us decide how much to eat? As yet, neither question can be answered fully. The first focuses attention on the nature and control of appetite and is much more difficult than the second, which raises the problem of the nature and control of hunger.

The brain unquestionably plays an important role in appetite control, just as, in mammals, this organ is now known to control the *amount* of food eaten. According to an early popular hypothesis, the stomach was believed to regulate the quantities of food consumed. Muscular contractions of an empty stomach were thought to give rise to sensations of hunger, and a hungry animal was assumed to eat until its stomach was filled. Such filling then was believed to stop the hunger pangs, hence also food intake. But this hypothesis, still widely quoted among nonbiologists, turned out to be untenable

long ago. For even after surgical removal of the entire stomach, hunger sensations nevertheless continue to come and go as before. Moreover, a "stomach hypothesis" of hunger control does not account for chronic overeating or undereating.

A better explanation has emerged from experiments which have revealed the existence of special eating-control centers in the mammalian brain. In a brain region known as the hypothalamus (Chap. 18), two such centers have been identified. One is a hunger center. When it is stimulated, it sends out nerve impulses to various parts of the body, which cause the animal to eat. The other is a satiety center which, when stimulated, makes the animal refuse food. In test rats, tiny electrodes have been used to stimulate one or the other of these centers continuously. The result of such tests has been that the treated animals either overeat and become extremely obese or undereat and starve amidst a plentiful food supply. Evidently, the amount of food a mammal normally eats is determined by the commands the hunger and satiety centers send to the body.

But how do these centers decide whether to send a command "Eat" or a command "Do not eat"? Experiments have shown that blood glucose is the critical agent which stimulates one or the other of the eating-control centers. As we shall soon see, glucose circulating in the blood is a very sensitive indicator of the hour-by-hour nutritional state of the body. Shortly after a meal, the glucose concentration in the blood tends to rise. Long after a meal, blood-glucose levels tend to fall. If blood reaching the brain contains too much glucose, then the satiety center probably becomes selectively sensitive to this high glucose level and issues the command "Do not eat." Conversely, low glucose levels probably stimulate the hunger center selectively, resulting in the command "Eat" (Fig. 11.3).

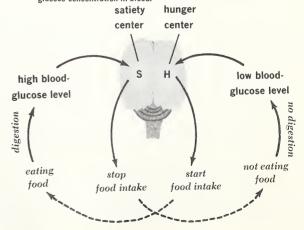
It should be clear that any condition which directly or indirectly influences glucose delivery to the brain, or affects the operation of the brain centers as such, is bound to affect food intake. Dozens of such conditions may actually do so. Proper

glucose delivery depends, for example, on normal digestive processes, normal liver function, normal blood circulation, and normal hormone balances, all of which, as we shall see, affect glucose metabolism profoundly. If, through disturbances in any of these functions, the brain receives consistently false information about the actual glucose supplies in the body, then consistent overeating or undereating may result.

Moreover, the brain centers are themselves subject to faulty operation. And they are influenced by a large variety of psychological factors, by reflexes, and by habits of long standing. They are also influenced by inherited genetic constitution, which, in the final analysis, governs the detailed operation of the body in all its aspects. Clearly, if the brain centers receive correct information but interpret it incorrectly, or interpret correctly but send out faulty commands, then abnormal food intake may again be the result.

We note that whether or not to eat, a seemingly simple decision, actually is determined by a multi-

FIG. 11.3. The control of food intake. Desire or lack of desire for food is governed by the satiety (S) and hunger (H) centers of the brain, which in turn respond differentially to the glucose concentration in blood.



tude of interdependent, interacting internal processes. And it is not surprising that, as is well known, practically *any* disturbance of *any* body function leaves its mark on food intake.

Granting now that desired kinds and appropriate amounts of food are being ingested, what happens to such food in its passage through the alimentary canal?

Digestion: enzymes

Digestion in different parts of the alimentary tract is achieved either by *mechanical* means or by *chemical* means, or by both. Mechanical digestion, carried out mainly by teeth, tongue, and the muscular grinding action of the stomach, achieves a progressive physical breakdown of bulk food. In parallel with this, chemical digestion occurs.

No matter where they occur, or what foods are involved, all instances of chemical digestion are reactions of the same common type: enzymatic hydrolysis. "Enzymatic" implies that the reaction is accelerated by an enzyme, and "hydrolysis," that the reaction is one of dissolution or decomposition, water being the dissolving agent. A generalized digestive reaction may be written

$$\mathbf{food} + \mathbf{H_2O} \xrightarrow{\mathbf{enzyme}} \mathbf{food} \ \mathbf{components}$$

In most animals, digestive enzymes are extracel-lular enzymes; that is, they are produced within cells but they are secreted and function outside cells. This puts them into a special category, for virtually all other enzymes in an organism are intracellular and function within cells. Moreover, digestive enzymes are relatively unusual also in that many of them may act on entire categories of chemicals. For example, digestive lipase promotes the decomposition of fat into fatty acids and glycerin:

$$\begin{array}{c} \text{lipase} \\ \text{fat} + \text{H}_2\text{O} \xrightarrow{\quad \quad } \text{fatty acids} + \text{glycerin} \end{array}$$

Here the lipase may be effective with any kind of fat, regardless of which specific types of fatty acids a

fat is composed of. Analogously, certain proteinand carbohydrate-digesting enzymes decompose many different kinds of proteins and carbohydrates, respectively. By contrast, most other, intracellular enzymes are highly specific, and each is effective only in reactions involving one particular type of molecule (Chap. 6).

Note, finally, that digestive breakdown of a food molecule is the exact reverse of the synthesis of that molecule. For example, the digestion of fat yields fatty acids and glycerin; the synthesis of fat requires the joining of fatty acids and glycerin. In general,

$$X + \text{H}_2\text{O} \xrightarrow{\text{(enzymatic hydrolysis)}} \text{parts of } X$$

$$\xrightarrow{\text{(enzymatic dehydration)}} \text{parts of } X$$

$$synthesis$$

The *same* enzyme promotes the reaction in either direction, for, as we have seen in Chap. 6, an enzyme does not determine the direction of a chemical process.

The principal places where enzymatic digestion occurs are mouth, stomach, and small intestine. At each of these sites, one or more digestive juices are secreted by specialized digestive glands. Thus the salivary glands produce saliva, which acts in the mouth and, carried along by food, also in the stomach. The stomach wall secretes gastric juice, which again acts right there. The pancreas produces pancreatic juice, and the liver produces bile. Both of these flow through ducts into the small intestine, where they act in conjunction with intestinal juice (Figs. 11.4 and 11.5).

The digestive enzymes present in these various juices are of three general kinds, namely, carbohydrases, lipases, and proteinases. In other words, digestive juices may decompose complex carbohydrates, fats, and proteins. Note that a given digestive juice may contain not only enzymes, but also other chemicals which serve various digestive functions. For example, gastric juice contains strong hydrochloric acid, which macerates food and so aids in mechanical digestion. Which digestive juices con-

tain what enzymes and other constituents is shown in Table 7.

In the process of chemical digestion, carbohydrates present in bulk food are gradually decomposed into monosaccharides, e.g., glucose, fructose, and other six-carbon sugars. Whole proteins are broken up into individual amino acids. And whole fats are physically subdivided, through the emulsifying action of bile salts, into colloidal fat droplets. Some, but not all, of these droplets are also decomposed chemically into fatty acids and glycerin (Fig. 11.6).

Thus, at the completion of digestion, the intestine contains water in which are dissolved mineral ions and monosaccharides, amino acids, fatty acids, glycerin, and vitamins (which have not been affected by digestion). Also present are colloidal fat droplets, plus undigested or indigestible material. The last will be egested, and all other materials will be absorbed.

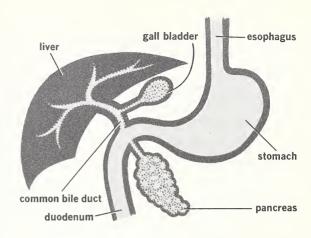


FIG. 11.4. The duodenal region; diagrammatic.

TABLE 7. The composition of various digestive juices*

	Saliva	Gastric juice	Intestinal juice	Bile	Pancreatic juice
рН	Slightly acid or basic	Strongly acid	Basic	Basic	Basic
Carbohydrases	Amylase, maltase		Amylase, disaccharases		Amylase
Proteinases		Pepsinogen, rennin	Peptidases		Trypsinogen, chymotryp- sinogen, peptidases
Lipases		Lipase	Lipase		Lipase
Other components		HCl (H+, Cl-)	Enterokinase	Bile salts, bile pigments	

^{*}Note that pepsinogen, trypsinogen, and chymotrypsinogen are inactive proteinases, secreted in this form. They are converted into active enzymes when they reach the cavity of the alimentary tract. Hydrochloric acid converts pepsinogen into active pepsin; the catalytic substance enterokinase converts trypsinogen into active trypsin; and trypsin itself converts chymotrypsinogen into active chymotrypsin. Carbohydrases and lipases are immediately active as secreted. For the specific action of digestive enzymes, see Fig. 11.6. Rennin curdles milk; i.e., it converts the milk protein caseinogen into the coagulated form casein.



FIG. 11.5. Cross section through the wall of the duodenum. The cavity of the gut is toward the top. Underneath the folded inner surface tissues of the gut, note the glandular layer. Its secretion is discharged into the gut cavity and contributes to the composition of intestinal juice. (General Biological Supply House, Inc.)

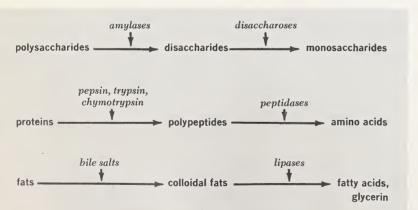


FIG. 11.6. Summary of enzymatic digestion. Polypeptides are partial breakdown products of protein. If they are allowed to act long enough, proteinases, and also amylases, may digest foods completely; proteinases may yield individual amino acids, and amylases, individual monosaccharides. Bile salts act physically, not chemically: they emulsify fats, i.e., they reduce large fat droplets into tiny droplets of colloidal dimensions.

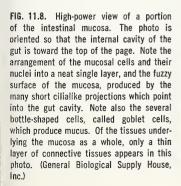
ABSORPTION AND EGESTION

As a food solution begins to be formed during digestion in the intestine, this solution is kept constantly moving and churning. The muscles of the intestinal wall (Fig. 11.7) tend to constrict behind a given volume of food and to relax in front of it. Waves of such muscular activity may sweep along whole sections of intestine, and these waves, called peristalsis, move food along and keep it agitated. A peristaltic wave may sweep forward for a short distance at some section of the small intestine, then may stop, and another wave may traverse the same or an even longer section. Stationary contractions may occur. Whole loops of the intestine may contract and shift and slide over other loops. Then forward peristalsis may again take place. As these movements proceed all along the gut, they bring food thoroughly into contact with the interior surface of the gut.

This surface is greatly folded and is studded with millions of near-microscopic villi, fingerlike protrusions which produce a velvety, carpetlike texture. Covering this whole inner surface of the gut is a single layer of cells, the intestinal mucosa (Fig. 11.8). By virtue of the folds and the villi, the surface area of the mucosa is exceedingly large. And the



FIG. 11.7. Abdominal dissection, man. A few of the coils of the small intestine are shown in the right portion of the photo; parts of the thicker large intestine are on the left side and just above the small intestine. Note that what appears on the left in the photo is on the right of the body. (Photographic Department, Rhode Island Hospital.)



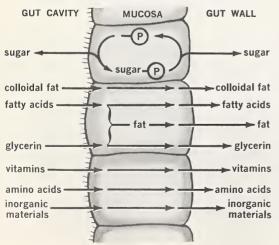


villi move continuously from side to side, stirring the food solution additionally and circulating it thoroughly about the mucosal lining.

Such churning of food by peristalsis and the action of the villi is advantageous for two reasons. First, churning mixes and remixes food with the digestive juices, allowing the chemical breakdown of virtually all potential food substances present. Second, agitation brings food into contact with different regions of the intestinal lining, a necessary condition if thorough absorption of food is to occur. The large area of the lining clearly facilitates this.

Absorption brings about a transfer of usable nutrients into the circulating fluids of the body. namely, the blood and lymph. A few substances, alcohol, for example, can be absorbed through the stomach wall, but most foods are absorbed through the intestine. Here nutrients must first be transferred from the gut cavity into the cells of the mucosa, and these lining cells then must release the

FIG. 11.9. The pattern of absorption of molecular nutrients through the intestinal mucosa. Note that absorption of sugars involves chemical reaction. This is also true for fatty acids, which combine chemically with bile salts during absorption. In other cases, absorption requires physical diffusion, though the occurrence of chemical reactions is not ruled out.



food molecules into the deeper parts of the gut wall, where blood and lymph vessels are situated.

In this nutrient transfer from gut cavity into the circulating fluids, it was long thought that physical diffusion of molecules accounted for events adequately. But as in other situations where living membranes permit passage through them, passive diffusion is now known to be only a small part of the story. For the cells of the gut wall, like the cells of the root epidermis in plants, are active, selective. energy-consuming, and poison-sensitive, and they do work in transferring nutrients through them. They behave as if they "recognized" different chemicals. and they let some through but not others. For example, the three six-carbon sugars glucose, fructose, and galactose, all have molecules of the same size and atomic composition, namely, C₆H₁₂O₆. Thus they should diffuse equally fast through the gut wall, but they do not: fructose goes through most rapidly, galactose least rapidly. Evidently, simple diffusion is not the answer here. Indeed, it is now known that specific chemical reactions occur when given nutrients pass through the gut wall. For example, six-carbon sugars like glucose cannot be absorbed as such. They are first combined with phosphate groups (-P), and only such phosphorylated sugars may pass through the mucosa. On the other side, the phosphate groups are removed again, and what enters the blood stream is free sugar once more. Similarly, the absorption of fatty acids appears to involve a chemical combination of fatty acids with bile salts, and such fatty acid-bile salt complexes then pass through the gut wall (Fig. 11.9).

During the 4- to 8-hr stay of food in the small intestine, this organ absorbs most of the usable organic nutrients present in the gut cavity: monosaccharides, amino acids, fatty acids, glycerin, colloidal whole fats, and vitamins. Some water and some mineral nutrients are absorbed also, but most of the water and minerals travel farther into the large intestine, being absorbed primarily there.

The large intestine (Fig. 11.10), so called because of its wider diameter, is not only an absorbing organ but also an *excretory* one. For as water and minerals are absorbed, many waste materials and substances present in the body to excess are excreted from the blood into the cavity of the large intestine. This organ so aids in maintaining a properly balanced internal composition of the body. For example, the water-balancing action of the large



FIG. 11.10. Abdominal dissection, man. Portions of the large intestine are shown on the left of the photo and toward the top. The rounded termination of the large intestine, near left bottom, is the caecum, a blind pouch. Attached to it is the appendix (white arrow).

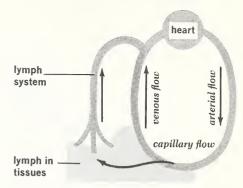


FIG. 11.11. The pattern of the lymph circulation of the body, diagrammatic. Fluid (lymph) escapes from the blood capillaries into the tissues of the body (large arrow at bottom of figure) and returns via lymph vessels into the blood circulation.

intestine is indicated in the familiar upset conditions of diarrhea and constipation.

The large intestine also initiates decay of indigestible and unabsorbable materials. This is brought about by dense, permanent populations of bacteria, which live in the gut as symbionts. These microorganisms obtain food from many of the materials the host cannot digest or absorb, and as a result of the nutritional activities of the bacteria, the substances in the large intestine undergo rapid decay. Frequently the bacteria release byproducts of their own metabolism, and some of these byproducts may be nutrients usable by the host. Vitamins are among these. Mammals actually obtain an appreciable fraction of their vitamin supply from the intestinal bacteria.

After passing through the large intestine, what is left of the original eaten food is largely *roughage*: tough fibers, gristle, pieces of cellulose, and unmacerated plant tissue, all suspended in more or less reduced quantities of water. Mixed with this are bile pigments, other excretions, bacteria and bacterial products, and whatever else may have been added or left over in the passage of food through the gut. These feces ("dregs") are in a more or less

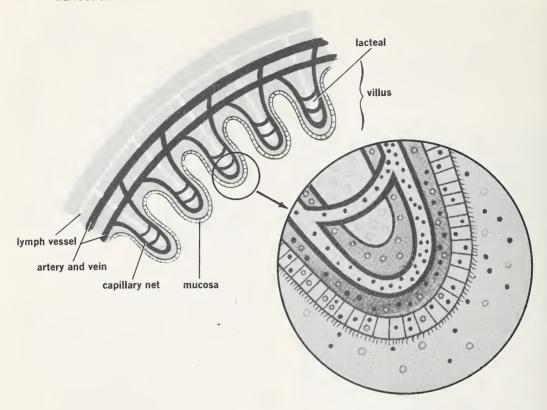


FIG 11.12. The villi of the intestine and a detailed diagrammatic representation of a single villus. Of the nutrients absorbed through the layer of mucosal cells, whole fats (open circles) collect in the lacteal of a villus and are transported from there through the lymph system. Other nutrients (black dots) are picked up by the blood stream.

advanced state of decay, and they are ultimately egested as semisolid masses.

The first phase of nutrition, alimentation, is now completed. Water, minerals, and the necessary organic nutrients have been absorbed, have been moved through the intestinal mucosa, and are ready now to be transported throughout the entire body.

THE TRANSPORT PATHWAYS

In each villus of the intestinal wall are small branches of the two transport systems of the body: capillaries of the blood-carrying circulatory system and capillaries of the lymph system.

The lymph system (Fig. 11.11) compensates for

the "leakiness" of the blood circulation. As blood flows in its closed network of vessels, it loses a certain amount of fluid through the thin walls of the capillaries. This escaped fluid, consisting principally of water, mineral ions, and molecular organic nutrients, is lymph, and it is responsible for the moist condition of all body tissues. Note here that a leaky blood circulation is not an instance of faulty engineering. On the contrary, fluid escape from capillaries is an adaptive necessity, for this is how the blood ultimately provides the cells of the body with water and all other necessary supplies.

But blood vessels would soon run dry if fluid losses were not made up. This is where the lymph system comes into play. Tiny lymph capillaries originate in all parts of the body, intestine included, and they pick up any free fluid in the tissues. Lymph capillaries then join into progressively larger, progressively fewer ducts, until a single large channel is formed. This channel empties into a vein

in the left shoulder region, and so it returns to the blood all the fluid lost originally.

In each intestinal villus, then, is a tiny capillary branch of the lymph system, called a lacteal, as well as a capillary loop of the blood circulation (Fig. 11.12). Foods are absorbed into these two channel systems in the following general pattern. The droplets of colloidal whole fat, plus some water and mineral ions, enter the lymph circulation via the lacteals. All other nutrients, including water, minerals, and vitamins, enter the blood circulation. The blood capillaries from the whole intestine eventually join into a single large blood vessel, the hepatic portal vein, and this vessel leads from the gut directly to the liver. Thus the transport system is so arranged that all absorbed foods, with the exception of whole fats, must travel from gut to liver via the blood. Whole fats bypass the liver, and they reach the general blood circulation of the body indirectly, via lymph (Fig. 11.13).

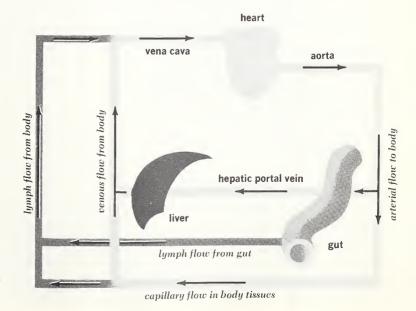
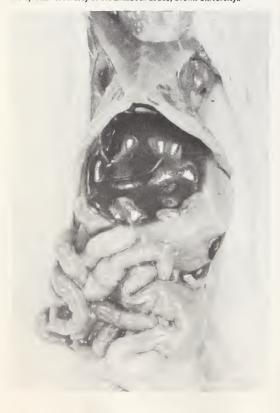


FIG. 11.13. Summary of the pathways of nutrient transport.

In those animals which possess a liver, this organ is an important food-processing and food-distributing station (Figs. 11.14 and 11.15). Foods received from the gut are variously transformed chemically, or stored, or sent out to all cells of the body via the blood. Through these activities, the liver ensures, regardless of when or how often the animal eats, that all cells receive an adequate mixture of all necessary foods, in adequate quantities. In a sense,

FIG. 11.14. Abdominal dissection, mouse. Note the liver just underneath the diaphragm. The stomach may be seen next to the liver on the left side of the body. The small tongue of tissue on the outer curvature of the stomach is a portion of the spleen. (Courtesy of Dr. Elizabeth Leduc, Brown University.)



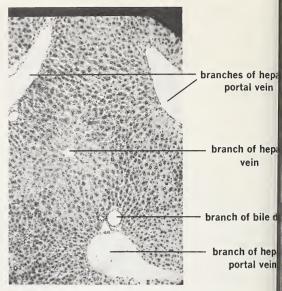


FIG. 11.15. Section through mouse liver, showing a functional unit of the organ. Blood from the intestine arrives through the branches of the hepatic portal vein, passes through the canallike spaces between liver cells, and collects in branches of the hepatic vein, from where it is distributed through the body. As blood flows past the liver cells, many vital metabolic exchanges occur. Bile secreted by liver cells collects in the branches of the bile duct. (Courtesy of Dr. Elizabeth Leduc, Brown University.)

the liver may therefore be regarded as a combination warehouse and traffic-control center. Whole fats evidently escape this control action of the liver, and they go directly to the cells of the body, in particular to the tissues which store fats.

Possession of a liver is highly advantageous. In plants, for example, or in animals without livers, internal food transport is direct from places of procurement to all other cells of the body. Hence if there is little or no procurement for a given period of time, the cells of the body must go without food. Where a liver is present, on the other hand, foods can be doled out to cells a little at a time, at a steady pace.

LIVER FUNCTION

As noted, carbohydrates reach the liver from the gut in the form of various monosaccharides. The liver transforms these into glycogen. This is a complex polysaccharide composed of many six-carbon sugar units, and it is the principal form in which carbohydrates are stored in animals. Thus glycogen is the animal equivalent of starch in plants. Glucose, in plants as in animals, is the principal form in which carbohydrates are transported and distributed. All animal cells, liver cells included, can convert glucose into glycogen, and vice versa. Normally, then, intestinal monosaccharides coming into the liver are converted to glycogen. From this store the liver subsequently produces glucose, and this glucose is sent in steady amounts to all cells of the body via the blood circulation (Fig. 11.16).

The blood glucose level is kept very constant by the liver. If that level should drop for any reason (e.g., too much is used by body cells), then the liver converts more stored glycogen into blood glucose. Conversely, if the blood glucose level should rise (e.g., too much glucose comes from the gut), then the liver stores the excess as more glycogen.

How does the liver carry out this regulating function? As noted, liver cells contain stored glycogen, and blood flowing through the liver past the cells contains glucose. Normally, the glycogen and the glucose are in chemical equilibrium; that is, glycogen is converted into glucose just as fast as glucose is converted into glycogen: glucose ⇒ glycogen. Under such conditions, no net change in the concentrations of either substance occurs. But if the glucose concentration in blood does change, because

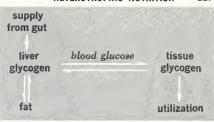
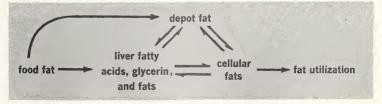


FIG. 11.16. The carbohydrate balance of the body.

more is supplied by the gut or more is used up in the body, then the chemical equilibrium will be disturbed. For example, if the blood glucose concentration should rise, then the conversion of glucose into glycogen will occur faster than the reverse conversion. As a result, glucose will be withdrawn from blood and liver glycogen stores will be increased. Conversely for a fall in blood glucose levels. These unequal rates of conversion will continue until the original chemical equilibrium is reattained. We note that the regulating action of the liver is largely a matter of maintaining and reattaining chemical equilibria.

The amount of glycogen the liver can store is not particularly large. Suppose more carbohydrates are eaten than are immediately needed by the body, and suppose also that the liver already stores glycogen to capacity. What happens to the excess carbohydrates? These are converted into fats, the liver also being an important fat store. Conversely, if so few carbohydrates are eaten that liver glycogen stores are reduced to zero (which may happen readily in carbohydrate-free diets), then some of the accumulated liver fat is converted to carbohydrates and through this source the liver may maintain normal blood glucose levels (Fig. 11.16).





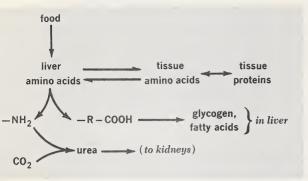


FIG. 11.18. The amino acid balance of the body. The splitting of amino acids into $-NH_2$ and -R-COOH fractions is called deamination.

The conversion of excess carbohydrates into fats is one source of the fat stores of the liver. Another is the fatty acids and glycerin which reach the liver from the gut. The liver recombines fatty acids and glycerin into fats, and whatever the source, liver fats may be sent via the blood to all cells of the body. There are other specialized places in the body where fats may be stored, e.g., under the skin, along membranes in the abdomen, and around the heart, kidneys, and other organs. These "fat depots" receive the colloidal whole fat which travels from the gut via the lymph. The liver and the fat depots communicate via the blood, and fats may be sent from any storage place to any other. Thus if the liver holds fats to capacity, any additional incoming supplies will be sent to some other fat depot. Conversely, these fat depots may replenish reduced liver stores. The cells of the body generally may be supplied with fatty nutrients either from the liver or from other fat depots, or from both sources (Fig. 11.17).

How does the liver deal with amino acids coming from the gut? In healthy adults, a normal diet usually yields more amino acids than the body needs. Amino acids are the foods from which tissue proteins are built up, and if an animal no longer grows and is not diseased, new tissue proteins are not required. What is required, vitally so, is daily repair of any tissue proteins which have become destroyed. We shall see later that a certain amount of breakdown of proteins (and all other tissue components as well) occurs all the time, even in a healthy individual. It is this normal destruction that body cells must counteract by building new proteins. For this, a certain small quantity of amino acids must be supplied daily through food. But eaten food is likely to supply far more than this requirement and, unlike carbohydrates or fats, amino acids are not stored. Hence the usual situation will be one of amino acid excess, and the liver handles this excess as follows.

We recall that amino acids, NH₂—R—COOH, contain amino groups, —NH₂. In the liver, any amino acids which are not passed on to body cells via blood are split apart chemically, such that the —NH₂ groups become separated from the rest of the amino acid molecules. This splitting process is called, appropriately, deamination. The resulting —NH₂ groups are then combined with CO₂, amply available in liver cells as a byproduct of respiration. Combination of —NH₂ and CO₂ yields a chemical called urea, and this is a waste material. It is carried away from the liver by the blood, and when it reaches the kidneys, it is excreted by these organs in urine.

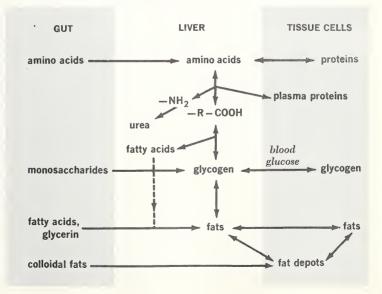
The other products of deamination, —R—COOH, or amino acids from which the —NH₂ groups have been split away, are not waste materials. On the contrary, these remnants contain organic carbon and hydrogen and oxygen, and they are converted by liver cells in some instances into carbohydrates, in others into fatty acids. These carbohydrates then join the glycogen stores of the liver, and the fatty acids, the fat stores. And since glycogen can be converted to fats, we may note that an animal may "get fat" not just by eating too many fats: too many eaten carbohydrates or too many eaten proteins eventually end up as fats also (Fig. 11.18).

The liver plays an important role in the distribution of several vitamins. Some vitamins absorbed from the gut are transported directly to tissue cells. However, others are taken up and collected by the liver and are released as the tissues require them. Vitamins A and D are in this category. The livers of fish store particularly large quantities of these vitamins; hence the nutritive value of, for example, cod liver oil. In certain instances, the liver also manufactures vitamins from nonvitamin sources. The pigment carotene, present in many foods, is not a vitamin. But when carotene reaches the liver, it may be transformed into active vitamin A.

In addition to these many storing and foodprocessing activities, the liver also performs numerous other, not necessarily nutritional, functions. For example, the liver destroys red blood corpuscles, and in the embryo it also manufactures them (Chap. 17). Moreover, other manufacturing processes are also carried out in the liver in which various kinds of nutrients serve as raw materials. Bile production is an example. Special liver products also include compounds which, like hormones, are vital for the maintenance of tissue cells but which are not available in food. It may be noted in this connection that the occasional inclusion of liver in the diet has long been known to be beneficial generally, and indeed necessary in certain diseases. The main activities of the liver are summarized in Fig. 11.19.

Thus, among the nutrients delivered to individual animal cells, are glucose; 23 different kinds of amino acids; fats, fatty acids, and glycerin; water and mineral ions; vitamins; and various special organic compounds. Being so supplied through the digestive and absorptive agency of the intestine, the regulative agency of the liver, and the transportive agency of blood, the animal cell, like the plant cell, may now see to the main business at hand: utilization of nutrients for survival. This means production of energy on the one hand and construction of new protoplasm on the other.

FIG. 11.19. The overall pattern of liver function, food distribution, and nutrient balances with respect to carbohydrates, fats, and proteins.



REVIEW QUESTIONS

- 1. Review the general nutritional pattern of animals, and contrast the nutrient requirements of plants and animals. For which materials are animals dependent on plants, and why? What is the basic function of an alimentary system?
- 2. Discuss the chemical aspects of digestion. What roles do enzymes play in digestion, and how are digestive enzymes distinct from others? What is the relation between digestion and synthesis?
- 3. What are intestinal villi, and what are their functions? How, and in what form, are different categories of food absorbed into the intestinal wall? What are the functions of the large intestine? What is the role of the intestinal bacteria?
- 4. If pure glucose were eaten, where would it be digested? Why are eaten vitamins, or orally administered medicines, not digested in the alimentary tract? Like vitamins, cellulose too is not digested in man; does the body handle vitamins and cellulose in the same way?
- 5. Describe the blood and lymph circulation through the intestine. Which food materials are carried away from the intestine by blood? By lymph?

- 6. What is the broad, general function of the liver, and what is the adaptive advantage of this organ? What happens to carbohydrates reaching the liver? What happens if carbohydrate supplies are exceedingly excessive?
- 7. By what processes is the constancy of the bloodglucose concentration maintained? Discuss several specific situations in which the blood-glucose level tends to change, and show how such tendencies are counteracted by the liver.
- 8. What is deamination? When, and where, does it occur, and what are the results of this process?
- 9. Can the liver manufacture carbohydrates and fats from derivatives of amino acids? Conversely, can the liver manufacture amino acids from carbohydrates or fats? Can the liver manufacture essential amino acids?
- 10. Describe the interplay between liver, fat depots, and body tissues in fat metabolism. Can an animal survive if fats are substituted for carbohydrates in its diet? Can an animal similarly survive in the converse situation?

SUGGESTED COLLATERAL READINGS

Bernard, C.: On the Mechanism of Formation of Sugar in the Liver, in M. L. Gabriel and S. Fogel, "Great Experiments in Biology," Prentice-Hall, 1955.

Boyd-Orr, I.: The Food Problem, Sci. American, vol. 183, 1950.

Mayer, J.: Appetite and Obesity, Sci. American, vol. 195, 1956.

Quisenberry, K. S.: The World's Principal Food Plants, Sci. Monthly, vol. 79, 1954.

Remington, R. E.: The Social Origins of Dietary Habits, Sci. Monthly, vol. 43, 1936.

Weaver, W.: People, Energy, and Food, Sci. Monthly, vol. 78, 1954.

CHAPTER 12

Gas exchange

Most organisms are aerobes; that is, their cells require oxygen for respiration. Also, respiration yields a byproduct, carbon dioxide, and this gas must be eliminated from the organism. Therefore, if a cell is to respire, it must not only be nourished with foods; it must also be provided with oxygen, and it must be rid of carbon dioxide. The acquisition of oxygen and the elimination of CO₂ are collectively called gas exchange or breathing. Breathing is a necessary aid to respiration, just as nutrition is a necessary aid. Note carefully here that breathing is not the same as respiration. Breathing includes all processes through which an organism carries external atmospheric gases to and from its individual cells. Respiration,

on the other hand, occurs within individual cells and constitutes the largely chemical process of energy production. Only cells respire; breathing by cells and organisms is a vital auxiliary process.

The breathing function and the structures serving it will be the subject of this chapter.

PATTERNS OF BREATHING

In the entire living world there are only five different patterns of gas exchange (Fig. 12.1). All five are governed by purely physical diffusion, such that O₂ and CO₂ always move from regions of higher concentration to regions of lower concentration.

By far the most widespread pattern is that of

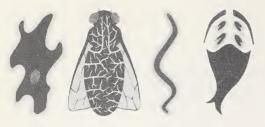




FIG. 12.1. The five principal patterns of gas exchange. From left to right: direct diffusion of gases through the cell surface (e.g., Monera, Protista, Metaphyta); tracheal tubes (e.g., insects); skin breathing (e.g., earthworms); gill breathing (e.g., fishes); and lung breathing (e.g., mammals). The surface for gas exchange in all but the insects is indicated in light gray.

direct exchange: each cell of an organism, be it unicellular or multicellular, individually picks up O₂ from the environment and releases CO₂ into the environment. This individual direct process occurs in all Monera, all Protista, all Metaphyta, and some Metazoa (e.g., sponges, coelenterates, flatworms). All these organisms are so built that every cell, or practically every cell, is in immediate contact with environmental water or air. Specialized breathing systems are therefore not needed and indeed do not occur.

Such systems do occur, however, in the majority of Metazoa, which are built so compactly that interior cells are *not* in direct contact with the environment. Of the four different patterns of gas exchange here encountered, one occurs in insects and some other arthropods. These animals possess hollow tracheal tubes, which begin at the body surface and lead into the interior. There they branch extensively, microscopic branch terminals reaching into all tissues. In effect, air is here piped from the outside to all interior cells, and gas exchange then can take place even deeply within the animal (Chap. 9).

In all other compactly built animals, gas exchange occurs across thin membranes. These are usually one cell layer thick, and they are exposed on one side to external air or water and on the other to blood vessels. Oxygen is absorbed into blood, and carbon dioxide is released from it. Thus the breathing membrane collects and releases gases, and blood *transports* them internally and distributes them to all cells.

The three principal variants of this pattern are

skin breathing, gill breathing, and lung breathing. Earthworms, for example, breathe exclusively through their thin, moist skins. Frogs use their skins too, but in addition, frog tadpoles possess gills and frog adults, lungs. In fish, crustacea, and many other aquatic animals, external water flows past gills and the gill membranes exchange gases. Many differently constructed gills are found in different aquatic animals, but the principle of operation is the same in all.

Lungs occur chiefly in terrestrial vertebrates. These breathing organs operate like gills, except that they are adapted to function in air instead of water. We shall examine the pattern of lung breathing in some detail, and as an illustrative example we shall use the specific pattern in man.

THE BREATHING SYSTEM

Structural components

Several familiar organs form the air channels of the breathing apparatus: nose and nasal passages, pharynx, larynx (or Adam's apple), trachea (or windpipe), and lungs.

The upper tract. The nasal passages are narrow winding pathways leading past intricately grooved and ridged walls (Fig. 12.2). Along the walls are found a number of paired openings. Some of these connect with the head sinuses, hollow air-filled cavities within some of the skull bones. For example, one large sinus is present in each of the two frontal bones which form the forehead.

Another pair of openings admits the contents of the tear ducts into the nasal passages. Tears are secreted continuously by glands in the outer corners of the eyes. The lymphlike fluid flows over, and so moistens, the surface of the cornea, then collects in the inner corners of the eyes and runs through the tear ducts into the nose (Fig. 12.3). Near the entry of the nasal passages into the pharynx, another two openings, one on the right, the other on the left, lead into the eustachian tubes. These pass into the middle-ear cavities. This connection permits the equilibration of air pressure between the external atmosphere and the middle ear, a space which is closed off from the outside by the eardrum.

Nasal passages, head sinuses, tear ducts, and eustachian tubes are lined with a continuous single layer of epithelial cells. Mucus secreted by them moistens the exposed surfaces. The epithelial cells in the nasal passages are ciliated, and some of these cells are specialized as odor receptors. Nerves lead from them to the nearby brain, where impulses are interpreted as smell.

Air passing through the narrow spaces of the nasal pathways is warmed and moistened, is freed of dust by the ciliated cells, which act as a filtering screen, and is smelled. As everyone is uncomfortably aware, inflammation of the passages, as in a cold or in hay fever, blocks air transmission to greater or lesser degree. The tissues swell up and obliterate the pathways. Increased secretion of mucus adds to the discomfort. Smelling is impaired. Tears overflow from the eyes, since the fluid cannot easily drain off into the blocked nasal chambers. And in severe cases, the inflammation may spread into the head sinuses, the middle-ear cavities, the throat, and the pathways leading from the throat to the lungs. Breathing by mouth under such conditions introduces relatively unwarmed, dust-laden, and unsmelled air.

The air and the food channel cross in the pharynx (Fig. 12.2). The esophagus is more or less collapsed in the absence of food, but some air may pass into it nevertheless. Most of the air enters the larynx through the glottis, a slit which can be

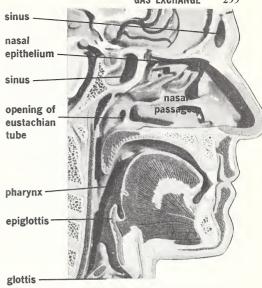
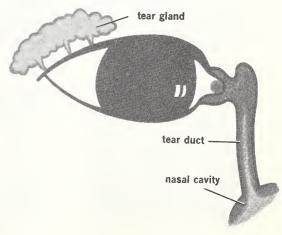


FIG. 12.2. The nasal passages and the upper parts of the breathing system. (Model designed by Dr. J. F. Mueller; photo. Ward's Natural Science Establishment, Inc.)





closed or opened to varying degrees. The larynx consists of a number of cartilages. Held together by membranes and movable relative to one another by muscles, these cartilages enclose a hollow cylindrical chamber. Attached to the inner surfaces of this chamber is a pair of horizontally placed fibroelastic ligaments, the vocal cords. These run from front to back in the laryngeal cavity, leaving an air passage in the mid-plane (Fig. 12.4).

Voice production. Sound is produced when air is expelled past the vocal cords through the glottis. The shape of the glottal opening and, as in a violin string, the length and tension of the vocal cords determine tone pitch. The shape of the larynx may be changed at will by muscles, and this in turn alters the tension of the cords. Taut ligaments vibrate rapidly and produce a highly pitched sound.

Also, notes are the higher, the shorter and thinner the vocal cords and the narrower the glottal slit. The volume of the sound produced depends on the force of the air blast and on the amplitude with which the cords vibrate.

A third characteristic of voice, tone quality, is influenced by the size and shape of the resonating cavities: chest, pharynx, mouth, and nasal passages. That tone quality changes as the position of lips, tongue, jaws, and cheeks is changed is familiar to everyone. Tone quality is altered also during a cold, or when the nose is pinched, or when sound is produced on inhalation, rather than on exhalation, as is normal. During puberty in males, the chest cavity and larynx enlarge and the vocal cords lengthen. The voice "breaks" as the individual learns to control his modified sound equipment. Deeper tones than in females are produced thereafter. The vocal

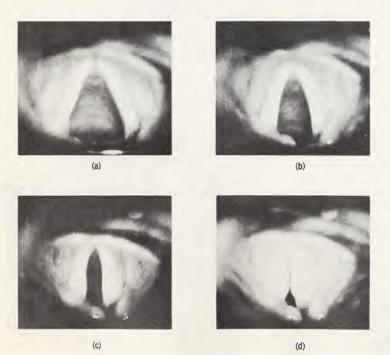


FIG. 12.4. The vocal cords of man. The view is from above, looking into larynx and trachea. From (a) to (d): sequence of vocal cord positions during the transition from quiet breathing to voicing. (Bell Telephone Laboratories, Inc.)

cords may thicken or scar during disease, or they may become encrusted with mucus during a cold, and a rasping voice is the result.

Most mammals make sounds of some sort. The giraffe is a notable exception. In birds, the only other vertebrate group with extensive, conspicuous voice capacity, sound is not produced in the larynx but in a syrinx. This voice box is located at the lower, not the upper, end of the windpipe.

The lower tract. The larynx is continuous with the trachea. This tube is prevented from collapsing by C-shaped rings of cartilage set horizontally into its wall. As in the larynx, the inner lining of the trachea is a ciliated, mucus-secreting layer of cells. The cilia beat upward, carrying mucus, dust, and occasional bits of food which "went the wrong way" into the pharynx. Air forced out as a cough facilitates the process.

At its lower end, the trachea divides into two bronchi, tubes having a smaller diameter than the trachea but the same structure otherwise (Fig. 12.5). Each bronchus subdivides after a distance into bronchioles, and each of the latter in turn branches repeatedly. Cartilage supports are not present in these smaller ducts. Also, their walls become thinner as they branch. Only the inner ciliated lining layer and some connective tissue containing elastic fibers are carried forward into the microscopic terminations of the branch system. Each such terminus is a raspberry-shaped sac made of a single layer of thin flat cells. This is an alveolus (Fig. 12.6). The sum of all alveoli constitutes the lung. The alveoli are held together by connective tissue, which carries nerves and a dense network of blood capillaries. The left and right parts of the lung are sculptured into lobes, their number corresponding to the number of main branches arising from the bronchi.

The lung on each side is situated in an intrathoracic space, which is bounded by two pleural membranes. The outer of these membranes lies against the diaphragm below, against the cavity holding the heart along the mid-plane of the chest, and against the rib cage at the top and along the

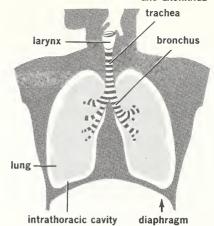


FIG. 12.5. The lower parts of the breathing system. Note that the intrathoracic cavity is sealed.

sides. The inner membrane covers the lung itself. Except for openings which admit the bronchi and the blood vessels to the lungs, the intrathoracic cavities are sealed off from the rest of the body. This feature is essential in breathing.

The breathing process

Air is moved through the breathing system by action of the diaphragm, the rib muscles, or both. The diaphragm produces what is called *abdominal breathing*, and the rib muscles, *chest breathing*.

The diaphragm separates the chest cavity from the abdominal cavity; stomach and liver lie directly underneath it. In relaxed condition, this thin muscular partition is dome-shaped. When it is contracted, the upward curvature of the dome disappears and the diaphragm flattens out. Such contraction pushes liver, stomach, and intestine downward and outward and so forces the belly out. Hence the designation "abdominal breathing." A flattening out of the diaphragm also enlarges the chest cavity, and this is the effective event in inhalation (Fig. 12.7). As a result of the enlargement, the pressure in the sealed intrathoracic space falls. This

microscopic branch of bronchiole

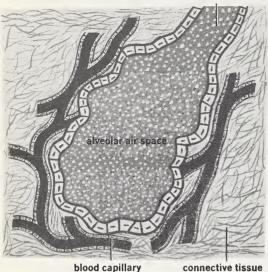


FIG. 12.6. An alveolus of the lung, surrounded by capillaries and connective tissue.

lowered pressure sucks the lung alveoli wide open. Air pressure within the alveoli consequently falls also, but this decrease is rebalanced instantly by air rushing in through the nose or mouth.

When the diaphragm relaxes, it resumes its original dome shape. The belly is pulled back, and the chest cavity, together with the intrathoracic space, reattains its former volume. Pressure within the intrathoracic space is then no longer lowered, and no further suction is therefore exerted on the alveoli. As a result, the elastic fibers which cover the alveoli recoil and air is pressed out from the lungs in an exhalation.

Breathing movements carried out by the rib cage have the same effect on the lungs as the above. Ribs are hinged to the vertebral column along the back and to the breastbone, or sternum, along the front. Attached between successive ribs are two layers of muscles, which raise or lower the rib cage. When the

chest is raised, the thoracic cavity expands and, through suction on the alveoli, inhalation occurs. A lowering of the chest results in exhalation. Chest breathing may enlarge the intrathoracic spaces much more than abdominal breathing; hence the former may produce deeper breaths than the latter.

Evidently, the mammalian method of breathing is a pressure mechanism. This knowledge has made possible procedures of "artificial respiration," often employed when injury or disease has incapacitated the automatic internal controls which maintain breathing normally. In artificial respiration by hand, or in "iron lungs," the chest is subjected to intermittent external pressure, which forces air into and out of the lungs just as does normal breathing.

In view of the importance of pressure, effective breathing clearly depends on the structural wholeness of the intrathoracic space. If the chest wall is pierced by a wound, external air enters the cavity on that side and the diaphragm or the rib muscles then can no longer exert suction on the lung. Hence the lung stays collapsed. In some diseases (e.g., tuberculosis), it is often desirable to rest one of the lungs. This is done by injecting air into one of the intrathoracic cavities, and the lung on that side collapses and becomes nonfunctional. The procedure may have to be repeated from time to time, for the injected air is gradually absorbed and removed by the blood circulation.

The control of breathing

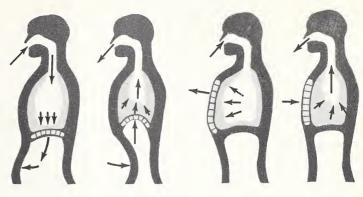
What maintains the bellowslike breathing movements year after year, without interruption, until life ebbs away? And what adjusts these movements in rate and depth to changing requirements? Breathing is maintained and regulated by a breathing center in the brain. This center is located in the medulla oblongata, the hind portion of the brain near the juncture of skull and neck.

The normal cycle. The breathing center responds to two kinds of incoming stimuli, one nervous, the other nonnervous. The nonnervous stimulus is carbon dioxide, present in blood at all times as a by-

expiration

inspiration





expiration

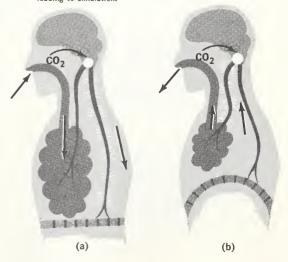
FIG. 12.7. The essential events in abdominal breathing and chest breathing.

product of cellular respiration. Blood-borne CO₂ accelerates the activity of the breathing center. The higher the CO₂ concentration, the greater the activity, and vice versa. This activity consists in sending nerve impulses to the breathing muscles, i.e., the diaphragm or the rib muscles. Special nerves conduct such impulses. For example, a pair of large phrenic nerves innervate the diaphragm. When impulses from the breathing center reach the breathing muscles, these contract, the chest cavity enlarges as a result, and the lung alveoli are sucked open. Air is then inhaled (Fig. 12.8).

The very stretching of the alveoli now stimulates special sets of nerves which originate in the alveolar walls. These nerves conduct impulses from the inflated lung to the breathing center. When such impulses arrive there, the center is *inhibited;* that is, the impulses override and suppress the stimulating effect of blood-borne CO₂. Consequently, the center ceases to send signals to the breathing muscles, and this prevents inhalation from going too far. For in the absence of signals from the brain, the breathing muscles relax. And as they do so, the chest cavity becomes smaller, the lung alveoli recoil to their original state, and air is exhaled (Fig. 12.8).

FIG. 12.8. The control of inhalation (a) and of exhalation (b). In (a) ${\rm CO}_2$ in blood stimulates the breathing center to send impulses to the diaphragm, leading to inhalation. In (b) impulses from the inflated lung inhibit the breathing center, leading to exhalation.

inspiration



After the alveoli have recoiled, they are no longer stretched, and the nerve endings in their walls therefore are no longer stimulated. Hence impulses cease to be sent to the breathing center, and the center consequently ceases to be inhibited. In the absence of inhibition, blood-borne CO₂ can again exert its effect. The breathing center now resumes its impulse transmission to the breathing muscles, and a new inhalation begins. The whole cycle is outlined schematically in Fig. 12.9.

Blood-borne oxygen also has an effect on the breathing center, but this effect is much less powerful than that of CO_2 and it probably plays only a minor role during normal breathing. We may conclude that a basic breathing rhythm is maintained by alternating, automatically self-renewing effects on the breathing center, produced largely by nervous inhibitions and carbon dioxide stimulations.

Variations in rhythm. It should follow that, as

the inhibitions and stimulations vary, so should the breathing rhythm. This is the case. As is well known, both the rate and depth of breathing can be altered easily. For example, an exercise of will, or powerful sensory and emotional experiences, may affect breathing greatly. These are nervous influences, relayed to the breathing center over many different and often indirect nerve paths.

Carbon dioxide produces modifications of the breathing pattern too. When the CO₂ concentration in blood is high, the rate of breathing is proportionately high, and vice versa. High CO₂ concentrations build up whenever the rate of CO₂ production through respiration is greater than the rate of CO₂ removal via the lungs. This is the case, for example, at the start of strenuous physical work, when intensified energy production in cells liberates increasing amounts of CO₂. By speeding up breathing under such conditions, CO₂ hastens its own removal through the lungs. Faster breathing at the same

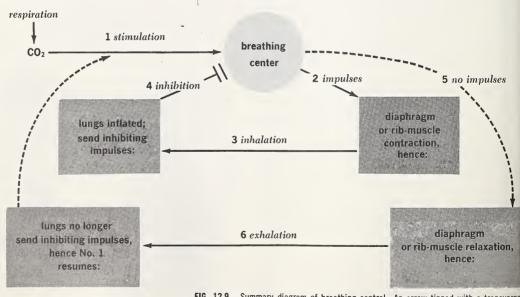


FIG. 12.9. Summary diagram of breathing control. An arrow tipped with a transverse double bar, as in 4, designates inhibition.

time increases the oxygen supply, just when the tissues require more oxygen.

The concentration of CO₂ in blood becomes extremely high when breathing is deliberately stopped altogether. But the accumulating gas then soon stimulates the breathing center so strongly that a resumption of breathing is *forced*, even against the most intense will. An animal cannot commit suicide by holding its breath.

Conversely, when the CO₂ concentration in blood is low, the breathing center is stimulated rather weakly and breathing slows down. This is the case during sleep or rest, when respiration and CO2 production are minimal. The extreme here is the overventilated condition, produced, for example, when breathing is intentionally made as deep and as rapid as possible. Carbon dioxide may then be exhaled so fast that abnormally little of the gas reaches the breathing center. A similar lack of CO2 and of oxygen may develop in the rarefied atmosphere at very high altitudes. Under conditions of this sort, the breathing center may temporarily cease to operate altogether and a "blackout" may ensue. Breathing will remain stopped until the CO2 concentration has again built up to a high enough level to stimulate the center adequately.

Breathing is a means to an end. The most immediate end is the procurement of additional oxygen and the removal of excess carbon dioxide. Fresh atmospheric air as inhaled contains some 20 per cent oxygen and 0.03 per cent carbon dioxide. Exhaled air includes only 16 per cent oxygen, but some 4 per cent carbon dioxide. Evidently, a fifth of the available oxygen has been retained in the body and more than 100 times the amount of carbon dioxide has been expelled. What happens to the one, and where does the other come from?

GAS TRANSPORT

Inasmuch as blood is the transport medium of the respiratory gases, an intimate association between circulation and breathing may be inferred. Indeed, the heart is virtually embedded in lung, and millions of blood capillaries ramify over the lung alveoli. Blood and air here approach each other very closely.

If blood is rich in oxygen, it is called <u>arterial blood</u>; if it is rich in CO_2 , it is called venous blood. An artery is a blood vessel leading *away* from the heart; a vein, a vessel leading *to* the heart. Note that the designation "artery" or "vein" does not depend on the kind of blood carried, but rather on the direction of blood flow within the vessel.

In all body tissues, cellular gas exchange takes place; cells take up oxygen from, and add carbon dioxide to, the blood. Here, therefore, blood becomes venous. This CO2-rich blood then travels to the heart, entering this organ via a vessel called the vena cava (Fig. 12.10). From the heart, venous blood is pumped through a pair of short pulmonary arteries into the nearby lungs. These arteries branch into extensive networks of capillaries, spread over the lung alveoli. Pulmonary gas exchange takes place here; CO2 leaves the blood, and O2 enters. Thus blood becomes arterial. This O2-rich blood now collects in a pair of pulmonary veins, which lead back to the heart. Redistributed from the heart via the aorta throughout the body, blood supplies new oxygen to tissue cells and is ready to carry off new carbon dioxide. That is the general pattern. How is it realized in detail?

The exchanges

The transfer of oxygen from the lung alveoli into the blood, and the reverse transfer of carbon dioxide, are governed primarily by <u>diffusion</u>. This is one of the very few instances where active cellular absorption and secretion do not play a role. The wall of an alveolus consists of a thin, single layer of cells, and the wall of a blood capillary also consists of such a layer. Neither of these walls offers resistance to the passage of gaseous O₂ and CO₂. Gas exchange may therefore take place much more rapidly than if absorption and secretion were necessary.

The specific direction in which the gases move is determined by the prevailing pressure gradients, or tension gradients, between blood and lung. Spe-

FIG. 12.10. The pulmonary circulation. Arterial blood is shown in dark gray, venous blood in light gray. Note that the left side of the body appears on the right in this diagram and the right side of the body on the left. Anatomical drawings are usually oriented as if observer and subject were face to face.

cifically, atmospheric air in the lungs contains only a little CO₂, but the venous blood which flows into the lungs from the body is virtually saturated with the gas. Hence the pressure, or tension, of CO₂ in blood is greater than that in the alveoli and a tension gradient points *out* of the capillaries. Carbon dioxide therefore moves in that direction, or better, more CO₂ molecules diffuse out of the blood than into it. As a result, blood ceases to be venous (Fig. 12.11).

The pressure pattern is the reverse with respect to oxygen. Blood flowing into the lungs from the body is oxygen-poor, for the tissues have removed much of the gas. But the air in the alveoli contains a maximal amount of O_2 . Hence a tension gradient points *into* the blood and more O_2 molecules diffuse into the capillaries than in the reverse direction. As a result, blood becomes arterial.

These interrelations explain why breathing is inefficient at high altitudes. In rarefied air, the atmospheric oxygen pressure is greatly reduced and the pressure differential between lung and blood is therefore low. Oxygen diffusion consequently does not take place as readily. We may similarly understand why the close atmosphere of an unventilated, overcrowded room makes breathing difficult. The CO₂ tension in the room is high, approaching that in blood. Hence CO₂ cannot easily leave the blood.

Just as in the lungs, cellular gas exchange in the body tissues is also governed by tension gradients (Fig. 12.11). Cells continuously use up oxygen in respiration, and the tension of this gas in cellular protoplasm is therefore low. The tension in arterial blood is higher, however; hence O₂ diffuses from blood into tissue cells. Blood consequently ceases to be arterial. At the same time, since respiratory CO₂ is produced in cells steadily, the CO₂ tension within tissue cells is high. But arterial blood has low CO₂ tensions, and the gas therefore diffuses from tissue cells into blood. This makes blood venous.

How are respiratory gases carried in blood?

The vehicle

Transport of respiratory gases requires a medium containing water, a number of inorganic ions, and red blood corpuscles.

The corpuscles owe their red color to hemoglobin. This complex pigment, customarily symbolized as Hb, consists of two parts, heme and globin. Heme resembles chlorophyll structurally, but it contains iron rather than magnesium. Heme is the active, functionally significant fraction of hemoglobin. Globin is a protein, which probably serves mainly as a carrier of heme.

Hemoglobin has the capacity of forming a loose chemical combination with oxygen:

$$Hb + O_2 \rightleftharpoons HbO_2$$

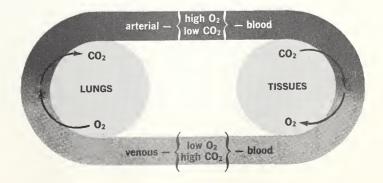
This reversible reaction will shift to the right when O₂ is present in excess. As we have seen, this is the case in the lung capillaries, and HbO₂, or **oxyhemoglobin**, forms there.

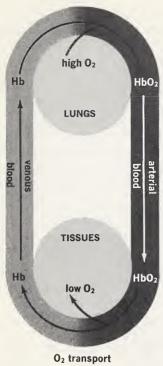
Oxygen is carried in blood largely in the form of HbO₂. A little oxygen also *dissolves* in the water of blood, in the same way as all atmospheric gases dissolve in water. Indeed, blood contains dissolved CO₂ and N₂ as well. When the external air pressure suddenly falls, as during rapid ascents into high altitudes or up from great depths, then the dissolved gases may fizz out of the blood in the form of bubbles. Dangerous "bends" may result. The effect here is rather like removing the cap of a bottle of soda; gases then fizz out too.

When oxyhemoglobin reaches the tissues, the reaction above shifts to the left. Cells are oxygen-poor relative to the blood, and HbO₂ "unloads" its oxygen. Free Hb forms again, and the free O₂ is taken up by the tissues (Fig. 12.12).

It may be noted that hemoglobin may transport not only oxygen but also carbon monoxide: $Hb + CO \rightleftharpoons HbCO$. This union is achieved much more easily than the union with oxygen. Hence, if carbon monoxide is present in the atmosphere, Hb becomes HbCO in preference to HbO_2 . This means that little oxygen can be transported to the tissues, which consequently cannot respire. Therein lies the poisonous effect of carbon monoxide.

FIG. 12.11. The exchanges of respiratory gases between the lungs and blood and between the body tissues and blood. Oxygen enters the blood in the lungs and leaves in the tissues. Carbon dioxide enters in the tissues and leaves in the lungs.





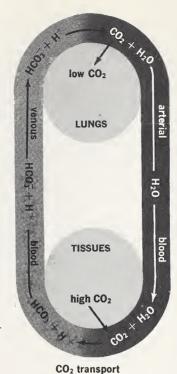


FIG. 12.12. The transport of respiratory gases in blood. Oxygen is carried in the form of oxyhemoglobin (HbO_2) , carbon dioxide in the form of bicarbonate ions (HCO_3^-) .

Of the CO₂ released from tissue cells, a small fraction dissolves physically in blood water, as already noted. Another small fraction combines with hemoglobin and is transported to the lungs in the form of HbCO₂. But the bulk reacts with water chemically and forms bicarbonate ions (HCO₃-):

$$CO_2 + H_2O \rightleftharpoons H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$
carbonic bicarbonate
acid ion

Inasmuch as tissue cells constantly add CO₂ to blood, this reaction proceeds to the right in the

tissues. Most of the CO₂ is therefore transported to the lungs in the form of HCO₃-. In the lungs, the conditions are reversed: CO₂ escapes into the alveoli, the reaction consequently shifts to the left, and more free CO₂ is released for exhalation (Fig. 12.12).

The processes auxiliary to cellular metabolism are now completed. Every cell of a plant or an animal has been supplied with oxygen, has been rid of carbon dioxide, and has already been provided with food. Hence it is ready to produce energy and to synthesize new protoplasm.

REVIEW QUESTIONS

- 1. Distinguish between breathing and respiration. How does gas exchange occur among plants? What are the principal patterns of gas exchange among animals?
- 2. Describe the structural organization of the breathing system in man. How is sound produced, and how can sound be varied in pitch, volume, and quality? What is an alveolus, and what is its relation to the lung? What chest structures surround the lungs?
- 3. Describe the pressure changes in the body associated with inhalation and exhalation in (a) abdominal breathing and (b) chest breathing.
- 4. How are inhalation-exhalation cycles controlled and maintained automatically? Review here the role of CO₂ and of the brain, and show by what sequence of events inhalation comes to alternate with exhalation.
- 5. Describe the processes through which breathing rate increases when physical exercise is begun and decreases at the onset of sleep.
 - 6. Describe the pattern of blood circulation through

- the body. Where, specifically, does venous blood become arterial and arterial blood become venous? In the circulation through the lungs, which blood vessels contain arterial and which contain venous blood?
- 7. By what processes does arterial blood become venous, and vice versa? Show what factors govern these changes, and describe the actual changes in lungs and tissues.
- 8. How is oxygen carried in blood? What reactions occur in the lungs and in the tissues? Why is carbon monoxide a poison?
- **9.** How is CO₂ carried in blood? What reactions occur in the lungs and in the tissues?
- 10. How are breathing and gas transport affected during ascent to high altitudes? How is nitrogen carried in blood? Why is breathing difficult in an unventilated room? What happens when a person holds his breath for a long time?

SUGGESTED COLLATERAL READINGS

- Baldwin, E.: "An Introduction to Comparative Biochemistry," Cambridge, 1949.
- Fox, H. M.: Blood Pigments, Sci. American, vol. 182, 1950.
- Williams, C. B.: Insect Breathing, Sci. American, vol. 188, 1953.

CHAPTER 13

Cellular metabolism: respiration

Nutrition and gas exchange are but means to an end. They supply the required ingredients with which each cell of each organism may carry out the main business of metabolism. This main business is energy production, or respiration, and energy utilization, which includes synthesis and other processes toward cellular maintenance and self-perpetuation.

Not every cell is specialized to aid in the nutrition and breathing of an organism—indeed, relatively few cells are; but every cell is specialized to respire and to synthesize. Moreover, these functions must be carried out at all times, uninterruptedly, if life is to be sustained.

The energy-producing phase of cellular metabolism is the subject of this chapter. We may note that whereas patterns of gas exchange differ among organisms and whereas patterns of nutrition differ even more, the basic pattern of respiration is the same in all cells of all organisms. Living creatures may be distinguished by many characteristics, but respiration is *not* one of these. This process has been inherited essentially equally and identically by all cells.

THE PATTERN OF RESPIRATION

Bonds and energy

Respiration may be defined as the liberation of chemical energy from organic molecules within living cells.

The last part of this definition, "within living cells," means largely mitochondria. The main phases of respiration take place in these specialized components of the cell cytoplasm. Virtually all complex cellular processes occur in distinct "factory" locations, and we have seen this to be so, for example, in photosynthesis. We may now note it to be the case also in respiration. To the mitochondria present in every cell flow all the necessary raw materials, and from them emerges usable energy. The electron microscope reveals that mitochondria have a complicated fine structure (Fig. 13.1). Much of the chemical machinery of respiration has been shown to be located along the walls of the internal mitochondrial partitions.

Concerning the remainder of the definition above,

"liberation of chemical energy from organic molecules," we may note that, directly or indirectly, the energy content of organic molecules represents <u>stored solar energy</u>. It is the sun which, through photosynthesis, makes possible the formation of primary organic molecules. All other organic materials are derived secondarily from these.

In photosynthesis, several inorganic molecules are combined into organic ones. In other words, the sun's energy is stored in the form of bond energies, which hold the atoms of a molecule together. Hence the locked-in energy may be released if, for example, the bonds between the atoms are broken. As much energy will then be liberated as was expended originally in making the bonds. Bonds need not always be broken outright to release energy. If they are merely weakened, then a fraction of the locked-in energy may be liberated too. Not all bonds contain the same amount of energy. The carbon-to-carbon bonds of organic molecules are particularly good sources, and we may note that respiration typically includes a breaking or a weakening of carbon-to-carbon bonds in fuel molecules.

FIG. 13.1. Electron micrograph of a single mitochondrion of a liver cell. Note the double bounding membrane and the internal membranous partitions. The chemical components of the respiratory machinery are situated along the membranes. (Courtesy of Dr. K. R. Porter, Rockefeller Institute.)



A similar process is very familiar from the nonliving world: burning. Fuels burned in a stove are principally wood, coal, oil, or "gas," and these too are organic materials containing stored solar energy. Energy liberation here is also a matter of breaking bonds. The principle involved is precisely the same as in respiration, and respiration, indeed, may properly be regarded as a burning. If this is so, why does respiration not produce the high temperatures of a fire?

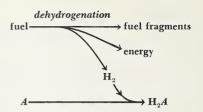
For two reasons. First a fire is uncontrolled combustion, in the sense that all the bonds within a fuel molecule may be broken simultaneously. A maximum amount of energy may then be released all at once. Such sudden, explosive release generates the high temperatures of a fire. Respiration, on the other hand, is controlled combustion. Energy is extracted from one bond at a time. If a fuel is respired completely, the total energy yield is the same as if it were burned in a stove, but in respiration the energy is liberated bit by bit, bond by bond. Hence temperatures stay low. Enzymes exercise the necessary control. Respiration is a series of enzymatic reactions, and biological combustion cannot take place any faster than the controlling enzymes will permit.

Second, the energy liberated in a fire is free energy—largely heat, and to some extent light. But in respiration only very little of the liberated energy escapes as heat and practically none as light. Instead, most of it is "packaged" directly into new chemical energy. As we shall see, fuel energy creates new chemical bonds, and it is in this form that metabolic energy is used in protoplasm. Since chemical bonds are not "hot," temperatures stay low during respiration.

Oxidation

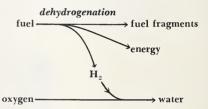
How is the chemical energy of a bond extracted? As we shall see, there are several ways. One of the most important, in respiration as in a fire, is with-drawal of hydrogen from the fuel, or dehydrogenation. This process requires the presence of a hydrogen acceptor. If we let A stand for such a

hydrogen acceptor, then combustion may be symbolized generally as follows:



Thus if a hydrogen acceptor is available, hydrogen can be withdrawn from a fuel. The carbon bonds of the fuel may break as a result, bond energy is thereby released, and the hydrogen can be collected and held by the acceptor.

Many different substances can and do serve as hydrogen acceptors. One which serves in fires, and in a major form of respiration, is atmospheric oxygen. Combustion in the presence of oxygen thus takes the general form



Water is a byproduct.

Note that hydrogen acceptors do not start combustion. They merely serve to collect and to remove the hydrogen "wastes." Note also that dehydrogenation is more or less synonymous with oxidation, whether oxygen or any other hydrogen acceptor is involved; in losing hydrogen, a fuel is said to become oxidized.

If it is not the hydrogen acceptor that starts combustion, what is? In a fire, the starter is *heat*. We must supply an initial amount of heat (by friction as in lighting a match, or through an electric spark, for example) to ignite the fuel, that is, to achieve a first dehydrogenation. Such heat energy,

applied from the outside, agitates the atoms of a fuel molecule to such an extent that hydrogen atoms begin to break loose. Enough energy is thereby released to initiate a self-sustaining chain reaction. Adjacent fuel molecules become agitated, their hydrogen atoms break loose, more energy is thereby released, new fuel molecules become agitated, etc.

In living protoplasm, respiration actually never starts, because it never stops. It is always under way, unceasingly. The "fire" of life was lit when life first originated, and since then it has been handed down from parent to offspring, without interruption. The continuing dehydrogenations are maintained not by heat but by enzymatic reactions. Special enzymes promote hydrogen removal from fuels, and special enzymes also act as primary hydrogen acceptors.

The fuels

What are the organic fuels in protoplasm? Anything that contains breakable carbon bonds-which means any organic constituent of protoplasm: carbohydrates, fats, proteins, their various derivatives, vitamins, other special compounds, and indeed all the innumerable substances which together make up protoplasm. Like a fire, respiration is no respecter of materials. Anything that can burn will burn, and in protoplasm this is the very substance of protoplasm itself. Respiration does not distinguish between the expendable and the nonexpendable. For example, an amino acid which is an important structural member of the framework of protoplasm, or is part of an enzyme, may be burned just as readily as an amino acid which has just arrived as a food.

However, if a fire is fed much of one fuel but little of another, more of the first is likely to be burned. Indeed, under normal conditions, a cell receives a steady enough supply of foods to make *them* the primary fuels rather than the structural parts of a cell. Also, some kinds of materials burn more easily than others, and some are more accessible to the fire than others. On this basis, foods,

carbohydrates and fats in particular, are again favored as fuels, and the finished components of a cell tend to be spared. Yet the sparing is relative only. The formed parts of a cell *are* burned gradually, including even those which make up the burning apparatus itself, i.e., the mitochondria.

But if protoplasm itself burns away, how can it remain intact and functioning? Only by continuous construction of new protoplasm, offsetting the continuous destruction through respiration. Note that these two processes go on side by side, at all times: destructive energy metabolism and constructive synthesis metabolism. One is in balance with the other, and foods serve both as fuel for the one and as building materials for the other. We say that the components of protoplasm are continuously "turned over"; that is, existing parts are continuously replaced by new ones. Protoplasm, we note, is never quite the same from instant to instant (see also Chap. 14).

The energy gain

What of the energy liberated in respiration? If it were to pass freely into the surroundings, it would become more or less useless metabolically. Evidently, an energy-trapping device is required. Such a device exists and is present in all cells. It consists of a group of chemicals collectively known as adenosine phosphates. Every cell contains at least two types of these: adenosine diphosphate, ADP for short, and adenosine triphosphate, ATP for short. As these names indicate, as many as three phosphate groups may be attached to an adenosine molecule. A molecule of ADP can be transformed into one of ATP by the addition of a third phosphate group, a process which requires energy. Conversely, ATP may become ADP by loss of one phosphate group and energy:

$ADP + phosphate + E \rightleftharpoons ATP$

Proceeding to the right, this reaction symbolizes the energy-trapping process of respiration. Energy liberated from a fuel molecule becomes incorporated into ADP and phosphate, and ATP is formed. Hence ATP is the chief endproduct of respiration. This important substance is also the energy vehicle; that is, it emerges from the mitochondria and diffuses to all locations within a cell where energy must be utilized. In utilization, the above reaction proceeds to the left: ATP breaks down, energy is released and used, and ADP and phosphate reappear.

In summary, therefore, respiration as a whole consists of three correlated events. *First*, a fuel molecule is oxidized, which means most often that hydrogen is removed from it. This hydrogen becomes attached to an appropriate acceptor, and if the acceptor is oxygen, water forms. This phase of respiration may be termed hydrogen transfer.

Second, as a result of hydrogen transfer, the carbon-to-carbon bonds of the fuel molecule may be broken. Smaller fuel fragments then form, and these may be oxidized and broken up in turn, until the original fuel has been degraded completely into one-carbon fragments. These always appear in the form of CO₂. This phase of respiration constitutes fuel breakdown.

Third, also as a result of hydrogen transfer, energy is released. A little of this energy escapes as heat, indicating that respiration is not 100 per cent efficient. However, most of the energy does not

become free in this manner but is harvested by ADP. ATP then forms, the main product of respiration. This phase may be called energy transfer. We may symbolize these three events as in Fig. 13.2.

This is the general pattern. Knowledge of it suffices for a basic understanding of respiration. If we wish to carry this understanding one step deeper, we may discuss each of the three phases of respiration in greater detail, as in the following.

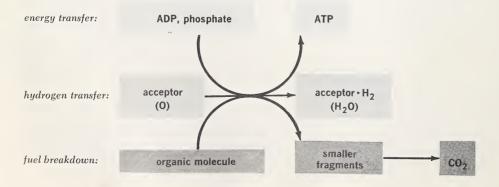
ENERGY TRANSFER

The pattern

We have just noted that the net result of respiration is a transfer of energy from chemical bonds in fuel into the chemical bonds of ATP. Why, then, respiration to begin with? If fuel energy already exists in the form of chemical bonds, what is the point of respiration if it only creates other chemical bonds?

Some bonds hold more energy than others. We may distinguish between high-energy bonds and low-energy bonds. To create the former a relatively large amount of energy must be expended, and a correspondingly large amount is released when such a bond is broken. However, most bonds in organic fuel molecules are of the *low*-energy type. For example, any of the carbon-to-carbon, carbon-to-

FIG. 13.2. The three main phases of respiration: energy transfer, hydrogen transfer, and fuel breakdown.



hydrogen, carbon-to-nitrogen, or carbon-to-oxygen links we have dealt with so far are low-energy bonds. If one of these is broken, only a little energy is released.

A critical dilemma now arises. On the one hand, available fuels provide only bond energies of low intensity. But on the other, very concentrated, intense packets of energy are needed for the synthesis of protoplasm, for muscular contraction, and for metabolic work in general. Fuels, as it were, provide energy of popgun intensity, but metabolic work requires cannons. What is needed, clearly, is an energy-intensifying process, one which would pool the many low-energy packets of a fuel molecule into a smaller number of high-energy packets.

Respiration does just that. It first concentrates the low bond energies of fuel and creates within a fuel molecule one or more high-energy bonds. This is the crucial event in oxidation, and in respiration as a whole. Then these high-energy bonds are transferred from fuel into the structure of ATP, a substance which is a high-energy carrier. Clearly, respiration accomplishes more than merely making new bonds out of old ones; it makes high-energy bonds out of low-energy bonds. And through ATP it supplies energy of uniformly high intensity to all points of utilization.

The creation of high-energy bonds from lowenergy bonds is achieved essentially by internal reorganizations of a fuel molecule. Each such molecule is characterized by a specific pattern of atoms, hence a specific pattern of bonds between the atoms. If a chemical change occurs, some of the atoms may change position, others may be removed, still others may be added. Whatever happens, the arrangement of the atoms will change and the pattern of the bonds will therefore change also. Many changes of this sort do not affect the content or distribution of the bond energies. But some do. And it may then happen that the original bond energies of the molecule become redistributed in such a way that one of the bonds comes to hold a great deal of energy whereas others hold even less than before. In effect, a high-energy bond will have

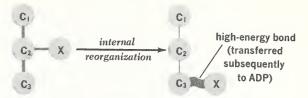


FIG. 13.3. Through internal reorganization of the atoms of a molecule, a high-energy bond may be created. Such a reorganization is an oxidative change.

been created at the expense of several low-energy bonds (Fig. 13.3).

If a molecular reorganization occurs which does redistribute the energy so that a high-energy bond is created, then we say that an oxidation has taken place. As already noted, the most important type of oxidative change is a dehydrogenation, that is, a removal of hydrogen from a fuel. Thus respiration will include events of the following general type:

fuel with low-energy bonds
$$\xrightarrow{Oxidation}$$
 fuel with high-energy bonds (1)

The process

The principal high-energy bond in metabolism is the **phosphate bond**, that is, the bond which joins a molecule to a phosphate group (—®). We have already encountered such —® groups earlier, e.g., in Chap. 10. Not all phosphate bonds are of the high-energy variety. But the properties of the phosphate bond are such that it can contain a great deal of energy, much more than is needed simply to hold —® to a molecule. In that case, the phosphate bond in effect stores extra energy; that is, it is a high-energy bond. To distinguish the high-energy bond, we use the symbol ~. Thus we may have either

A low-energy phosphate bond may be converted into a high-energy phosphate bond if more energy becomes concentrated in it. As noted above, such energy enrichment of a bond may be achieved by oxidation. Hence we may rewrite the general equation (1) above as follows:

Clearly, before such a reaction can take place, "fuel—P" must be available as a starting material. In other words, the addition of a low-energy—P group to a fuel molecule, or phosphorylation, will be an important preliminary step toward the creation of high-energy bonds. Respiration actually includes such preliminary phosphorylations, and the creation of high-energy bonds proceeds according to the following general sequence of events:

$$\begin{array}{c} \begin{array}{c} phospho-\\ rylation \end{array} & \text{fuel} - \textcircled{\mathbb{P}} & \overset{oxidation}{\longrightarrow} & \text{fuel} \sim \textcircled{\mathbb{P}} & (3) \end{array}$$

One final consideration completes this analysis of energy transfer. We know that the useful energy of the fuel is now concentrated in the high-energy bond of "fuel~P." It is this high-energy phosphate group which can be harvested as a net gain of respiration. As noted earlier, the substance ADP accomplishes the harvesting by transforming into ATP. The transformation requires a phosphate group and energy, and this is precisely what "fuel~P" can supply. The final energy transfer may therefore be written:

fuel residue
$$ADP + \neg P = ATP$$
(4)

In short, fuel∼® hands over its ∼® to ADP, which becomes ATP as a result. And as a further

result, the fuel may have broken up into smaller fragments. ATP now contains the original fuel energy, and ATP therefore may serve as an *energy donor* wherever energy is needed in a cell.

We may therefore recapitulate the entire energy aspect of respiration as follows. First, a given fuel molecule is phosphorylated. Then it is oxidized, resulting (1) in the liberation of hydrogen and (2) in the creation of a high-energy phosphate bond. Finally, the high-energy phosphate group is harvested by ADP, resulting (1) in the formation of ATP and (2) in the appearance of fuel fragments. Schematically,

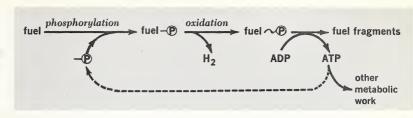
$$\begin{array}{c} phos-\\ phoryl-\\ ation\\ fuel \xrightarrow{} \\ \hline \\ -\mathbb{P} \end{array} \begin{array}{c} oxida-\\ tion\\ fuel \xrightarrow{} \\ \hline \\ H_2 \end{array} \begin{array}{c} trans-\\ fer\\ fuel \xrightarrow{} \\ \hline \\ ADP \end{array} \begin{array}{c} fuel \\ \hline \\ ATP \end{array}$$

Note here that the chief product, ATP, holds not only energy but also phosphate groups. Hence ATP may serve in a cell not only as an energy donor but also as a phosphate donor. This answers a question. For where, we may ask, does the phosphate come from that phosphorylates a fuel to begin with? The answer is that such phosphate comes very largely from ATP. In other words, some of the product of respiration must be funneled back to the beginning of respiration, to make more respiration possible at all. We may summarize as in Fig. 13.4.

Much more total ATP is formed by respiration than is needed to carry out the initial phosphorylations. Hence the dotted line in Fig. 13.4. But note that this small starting requirement of ATP comes under the general heading of "metabolic work" and is one of the uses to which ATP is normally put. Note also that when ATP gives up its phosphate group in this way, it also relinquishes its highenergy bond and so becomes ADP once more. This ADP may then be re-used when ATP is formed again.

What happens to the hydrogen which is removed

FIG. 13.4. Some of the high-energy phosphate in ATP gained through respiration is expended in preliminary phosphorylations which make more respiration possible.



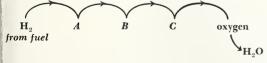
from fuel—P by oxidation? This leads to a consideration of the second of the three phases of respiration.

HYDROGEN TRANSFER

Aerobic respiration

We already know that dehydrogenation of a fuel requires the presence of a hydrogen acceptor. Atmospheric oxygen is an excellent acceptor. Yet fuels do not deliver H to oxygen directly. Moreover, oxygen may not always be available.

Fuels release hydrogen only to special organic acceptors of complex construction. Indeed, a whole series of such acceptors exists, and as in a bucket brigade, hydrogen from fuel is passed successively from one acceptor to the next, in fixed sequence. When oxygen is available, this gas functions as the *last* acceptor in the series, and H₂O then forms as a byproduct of respiration. If we let A, B, and C stand for different hydrogen acceptors, then the pattern of H transport to oxygen may be symbolized as follows:



We may ask why such a succession of carriers is required at all. Could not hydrogen be passed on to oxygen directly? Indeed it could, and that this is so can be demonstrated readily in the test tube. When such a test-tube experiment is performed, hydrogen and oxygen are found to combine explo-

sively. We should not conclude, however, that a similarly direct combination in cells would lead to explosion of cells. The quantities of gases involved here at any moment would probably be far too small to cause damage. The important conclusion is, rather, that the combination of hydrogen and oxygen is an energy-yielding process. And this undoubtedly explains the adaptive value of the succession of hydrogen carriers in cells. If hydrogen were to combine directly with oxygen, any energy released would appear suddenly, all at once. Most or all of it would then dissipate as heat and would become useless metabolically. But with a succession of carriers, the energy can be freed little by little, and this energy becomes useful. For when one carrier passes hydrogen to another, the carrier is in effect dehydrogenated. This is an oxidative change, and it yields usable energy trapped as ATP.

This production of ATP occurs in addition to any ATP already produced from fuel~P as discussed earlier. Hence there are actually two sources of ATP in respiration. One, as outlined previously, is the formation of fuel~P by oxidation and subsequent transfer of the ~(P) to ADP. The other source is the transfer of hydrogen from fuel to oxygen. The exact nature of this second source of ATP is still under study, but we may note that it too involves creation of high-energy phosphates and transfer of these to ADP. We may also note that of the total energy gained by the complete respiration of a fuel molecule, more ATP is actually produced through the second source than through the first. Hence the second source is the more important one. We may symbolize these two sources as in Fig. 13.5.

What are the actual hydrogen carriers between fuel and oxygen? There are three sets. The first set consists of two chemicals with rather long names: diphosphopyridine nucleotide and triphosphopyridine nucleotide. These are abbreviated as DPN and TPN. Both are manufactured in cells partly from one of the B vitamins, namely, nicotinic acid (niacin). Here is the reason why this vitamin is essential for life. All cells of all organisms must make or obtain nicotinic acid as a vital building material in the construction of DPN and TPN. These two hydrogen carriers accept H2 removed from fuel and then pass the hydrogen on to the second carrier in the series to oxygen. In some situations it is DPN, in others TPN, which functions as first carrier.

The second carrier is a chemical called flavoprotein. It is manufactured in cells from another B vitamin, namely, riboflavin, or vitamin B₂. Flavoprotein has the specific property of accepting H₂ from either DPN or TPN and then handing it on to the third set of carriers. This third set consists of a group of related materials collectively known as the cytochrome system. Cytochromes are red pigments, chemically related to hemoglobin of animal blood. But note that cytochromes occur universally in all cells, plant or animal. The properties of the cytochrome system are such that it may accept H₂

from flavoprotein and hand on the hydrogen to oxygen, the fourth and final acceptor. Because oxygen is needed in this form of respiration, it is called *aerobic respiration*.

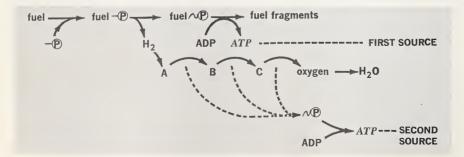
Including the sequence of hydrogen transfer, we may now symbolize respiration up to this point as in Fig. 13.6. Note that oxygen serves essentially as collector of a waste material, namely, hydrogen. Water forms as a result.

Anaerobic respiration

It should be clear that if hydrogen transfer as above is in some way made impossible, then aerobic respiration as a whole will become impossible. Actually, each step of the hydrogen-transfer chain can be blocked readily. For example, dietary deficiency of B vitamins will reduce or stop the availability of DPN/TPN and riboflavin; cyanide poisons the cytochrome system and prevents it from functioning; and choking prevents oxygen from reaching cells altogether. Any one of these conditions prevents hydrogen removal from fuel, hence production of ATP. And as respiration is stopped, death may occur quickly.

But to a greater or lesser extent, living organisms may have a way out. Indeed, certain bacteria today can live only in environments in which oxygen is absent; to them O_2 is actually a poison. (In this

FIG. 13.5. The two sources of ATP in respiration. One source is oxidation of fuel, and a second source is hydrogen transfer from fuel to oxygen.



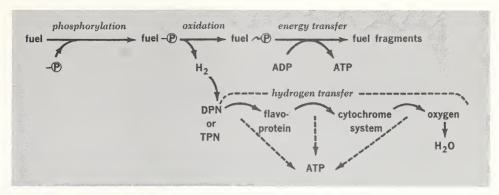


FIG. 13.6. Diagrammatic summary of aerobic respiration.

connection, we may recall that when life first began, atmospheric oxygen probably did not exist at all, and all organisms then must have survived without this gas.) Other modern organisms, notably some bacteria and fungi (e.g., yeast), can use O_2 if it is available, but if not, they can do without it. And all remaining organisms must have oxygen for survival, yet even a man may get along without the gas for 2 or 3 min.

Whenever oxygen supplies are inadequate, or whenever hydrogen transport to oxygen is otherwise blocked, organisms may respire in a way which does not require oxygen. This is <u>anaerobic respiration</u>, or fermentation, probably the ancient original form of energy production. Under conditions of oxygen deficiency, this anaerobic type of respiration may become a substitute or a subsidiary source of energy.

Anaerobic respiration is precisely the same as aerobic respiration up to the point where DPN accepts hydrogen from fuel. After this, fermentation clearly must follow a different course, for the present assumption is that the usual pathway to oxygen is blocked. The principle of fermentation is relatively simple: when the exhaust pipe of an engine is stopped up, the engine may still continue to operate if an alternative outlet for the waste gases

is available. Oxygen is the normal outlet for hydrogen, and if oxygen is unavailable, a final acceptor *other* than oxygen is used.

The alternative <u>hydrogen acceptor is pyruvic acid</u> $(C_3H_4O_3)$. As we shall see shortly, this acid is produced normally during the respiratory breakdown of carbohydrate fuels. If oxygen is amply available, pyruvic acid is merely one of the intermediate steps in the combustion of carbohydrates. In other words, it is a fuel which, in the presence of oxygen, may be burned further. But pyruvic acid happens to have the property of combining readily with hydrogen. Thus, if DPN cannot "unload" its hydrogen to flavoprotein, it *can* unload to pyruvic acid instead. The acid then ceases to be a fuel and becomes a hydrogen acceptor.

When pyruvic acid combines with hydrogen, the result is the formation of *lactic acid* in animals and some bacteria and of *alcohol* and CO₂ in plants and some Protista. Different enzymes promote these reactions in plants and animals, hence the difference in the endproducts. We may outline the whole process as in Fig. 13.7.

With these reactions, anaerobic respiration is completed. Since only carbohydrates normally yield pyruvic acid directly, fermentation will be most efficient when carbohydrates are available as fuels.

FIG. 13.7. Diagrammatic summary of anaerobic respiration.

The energy gained by fermentation is far less than that gained aerobically. First, with the path to oxygen blocked, the ATP normally created by H transfer to oxygen cannot be realized. Second, since pyruvic acid now functions as a hydrogen acceptor instead of a burnable fuel, all the potential energy still contained in pyruvic acid must remain unused. For these reasons, fermentation yields only about 10 per cent of the energy which could be obtained through aerobic respiration.

This small amount of energy suffices to sustain organisms like yeast. In most other organisms, the energy gained by fermentation is too small to sustain life for any length of time. If hydrogen transport to oxygen is blocked completely, cell death will occur quickly, even though fermentation is under way. However, fermentation may suffice to supplement aerobic respiration when energy demands are high. For example, during intensive physical activity among animals, the oxygen supply to the cells may be insufficient despite faster breathing and an oxygen debt will be incurred. Fermentation then proceeds in parallel with aerobic respiration, and a little more energy so becomes available. Lactic acid will accumulate as a result. particularly in the muscles, which bear the burden of physical work.

Muscular fatigue is associated with increasing accumulation of lactic acid. When the amount of acid becomes very high, fatigue may become so great that intense activity can no longer be maintained. During an ensuing rest period, faster breathing at first continues. The extra oxygen so inhaled helps to burn away the accumulated lactic acid,

which now may serve as a fuel in aerobic respira-

We note that, like alcohol in plants, lactic acid is a potential fuel which in the later presence of oxygen may be burned completely. The energy contained in the endproduct of fermentation therefore need not be permanently lost to an organism. It is harvested during the aerobic conditions of a rest period, when the oxygen supply is high relative to cellular requirements. With the gradual disappearance of lactic acid from the muscles, fatigue disappears, breathing slows down, and a normal oxygen-energy balance is then reestablished.

These accounts of energy transfer and hydrogen transfer set the stage for a discussion of the third phase of respiration, i.e., combustion of actual fuels.

FUEL COMBUSTION

The pattern

In the course of reorganizing internally and thereby acquiring high-energy bonds, a fuel molecule becomes changed chemically. Sometimes the change is not great and the basic structure of the molecule is not affected. But sometimes the oxidative change may bring about a splitting of the carbon skeleton of the molecule. High-energy bonds may form regardless of whether a molecule splits or not, but when a split does occur, fragments with shorter carbon chains result. These are still energy-yielding fuels. Sooner or later, they in turn may be split into still shorter chains. Eventually, fragments will arise which contain but a single carbon atom each.

This final one-carbon breakdown product emerges

from respiration in the form of CO₂. Carbon dioxide represents the end condition of all metabolic fuels, and when a fuel has been degraded this far, all extractable energy has already been extracted. Complete degradation of a fuel to CO₂ can occur only in the presence of oxygen.

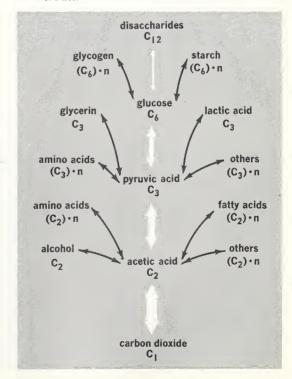
If we follow the sequence of fuel breakdown backward, then the next-to-last fuel fragment should consist of *two* linked carbons. This is the case. The fundamental molecule representing the two-carbon stage in respiration is acetic acid (C₂H₄O₂). In other words, progressive breakdown eventually transforms all fuels to acetic acid, and this two-carbon acid then transforms to one-carbon CO₂.

The manner in which the acetic acid stage is reached differs for different types of fuels. For example, many carbohydrates are first broken up into three-carbon compounds. Carbohydrates often contain whole multiples of three carbons. Photosynthesis yields a three-carbon endproduct, and more complex carbohydrates are built up from such units. This holds for glucose and all other six-carbon sugars, for twelve-carbon disaccharides, and for polysaccharides such as starch and glycogen. When any of these are used as respiratory fuels, the original three-carbon units reappear in the course of breakdown. Many other organic substances, glycerin, for example, are three-carbon molecules to begin with. All such C₃ compounds are eventually converted to pyruvic acid (C3H4O3). This acid is the common representative of the three-carbon stage in respiration. Pyruvic acid subsequently loses one carbon in the form of CO2 and so becomes acetic acid.

Fatty acids and related molecules consist of long even-numbered carbon chains. These do not break up into three-carbon units, but become two-carbon units directly. Other fuels are two-carbon molecules to begin with, and all such C₂ compounds eventually appear as acetic acid. Amino acids break down partly to pyruvic acid (which subsequently becomes acetic acid), partly to acetic acid directly. This holds also for many other organic substances which may happen to be used as fuel.

Thus the overall pattern of aerobic fuel combustion may be likened to a tree with branches, or to a river with tributaries (Fig. 13.8). A broad main channel is represented by the sequence pyruvic acid \rightarrow acetic acid \rightarrow carbon dioxide. Numerous side channels lead in this sequence, some funneling into the three-carbon pyruvic acid step, others into the two-carbon acetic acid step. The side channels themselves may be long or short, and each may have smaller side channels of its own. In the end, the flow from the entire system drains out as one-carbon carbon dioxide.

FIG. 13.8. Some of the main pathways in the aerobic combustion of fuels. Pyruvic acid, acetic acid, and carbon dioxide form a main sequence which other pathways join, like branches of a tree.



In any of these breakdown sequences, the reaction pattern is essentially as discussed earlier. A fuel molecule is first phosphorylated, then oxidized, and then ATP is harvested. The resulting fuel fragments still are fuels, which are again phosphorylated, then oxidized, and then de-energized by formation of ATP. These processes occur repeatedly, until only CO₂ is left. During such reaction sequences, also, hydrogen is removed at several points, and all this hydrogen is transferred by the carriers to oxygen.

The actual chemical details of fuel breakdown are exceedingly complex. However, we may still obtain a good understanding of the basic pattern by considering only a highly simplified and abbreviated account, in which attention is directed solely to numbers of carbon atoms and phosphate groups.

Carbohydrate breakdown

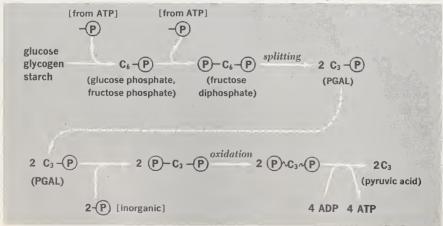
As noted above, if carbohydrates are used as fuels, they are burned first to three-carbon pyruvic acid. In this process, polysaccharides and monosaccharides of all kinds are first converted into phosphorylated six-carbon units; that is, carbohydrate fuels

with long carbon chains are split up into C_6 fragments and to each such fragment a phosphate group is attached. We may symbolize the result as C_6 — \mathbb{P} . If glucose, a C_6 unit to begin with, is a fuel, it is similarly phosphorylated to C_6 — \mathbb{P} . The subsequent transformations of these C_6 — \mathbb{P} units are outlined in Fig. 13.9.

This figure shows that the reaction sequence consists, first, of successive further phosphorylations; i.e., $-\mathbb{P}$ groups become attached at *each* end of a C_6 chain. Then the chain splits into two C_3 chains, and more $-\mathbb{P}$ groups are attached to the free ends of these C_3 chains. Second, in successive oxidations, all $-\mathbb{P}$ groups now present are transformed into $-\mathbb{P}$ groups. And third, these high-energy phosphates are transferred to ADP. What is then left of the original fuel is a C_3 compound, namely, pyruvic acid, or $C_3H_4O_3$.

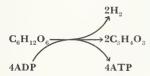
Note here that one of the intermediate steps in breakdown is PGAL, which is also the principal endproduct of photosynthesis. Thus, when a plant cell creates photosynthetic PGAL, this molecule may be respired immediately to pyruvic acid,

FIG. 13.9. Abbreviated summary of the respiratory degradation of carbohydrates to pyruvic acid. The formulas for chemicals are incomplete, showing only numbers of carbon atoms and phosphate groups.

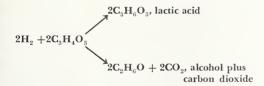


through the reactions to the right in Fig. 13.9. Alternatively, photosynthetic PGAL may be transformed to glucose or starch, and this occurs through the reactions to the left in Fig. 13.9, the sequence proceeding in reverse. Virtually all reactions in metabolism are fundamentally reversible, and whether they go in one direction or the other depends on conditions. In respiration, conditions are such that the reactions proceed preferentially in the direction of the arrows in Fig. 13.9.

If we assume that the starting fuel is one molecule of glucose, $C_6H_{12}O_6$, then we note that it is broken up into $2C_3H_4O_3$, pyruvic acid. In the process also, $2H_2$ are released and 4ATP are produced. In summary,



If respiration is *anaerobic*, the $2H_2$ will be accepted by the two pyruvic acid molecules formed and respiration will be completed:



Four ATP molecules will then represent the gross energy gain. The net gain is smaller, for as outlined earlier, some of this ATP must be used in the phosphorylations at the start of the whole breakdown sequence.

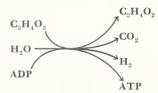
On the other hand, if respiration is aerobic, the $2H_2$ will be transferred to oxygen, more ATP will be formed by this transfer, and the pyruvic acid remains free to be burned further.

This further breakdown of pyruvic acid is not

unique to carbohydrates. For as we have seen above, other fuels become pyruvic acid also. Certain amino acids, for example, or glycerin, each converts to pyruvic acid through its own special breakdown sequence. Thus, with the formation of pyruvic acid, from any original fuel source, we have reached the "main stream" of respiratory breakdown from \mathbf{G}_3 to \mathbf{G}_2 to \mathbf{G}_1 .

C_3 to C_1

Pyruvic acid becomes acetic acid through a series of phosphorylations and oxidations in which hydrogen is again removed and ATP is again formed. This conversion from C_3 to C_2 also involves the release of a one-carbon fragment, in the form of CO_2 . Vitamin B_1 , or *thiamine*, is one of the agents needed in this removal of CO_2 from pyruvic acid. Hence the universal requirement of this vitamin for the survival of every cell. In greatly abbreviated and simplified form, the formation of acetic acid may be described by the following statement:



Note that water is a raw material. Of the products, H₂ is transferred to oxygen, CO₂ escapes into the environment, ATP represents the energy gain, and the molecule of acetic acid is still a fuel which can be burned further.

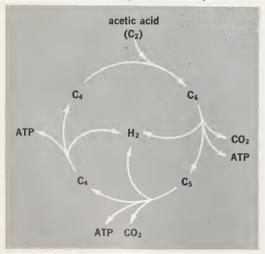
The acetic acid stage is a main collecting point in respiration, into which funnel many separate breakdown sequences. For example, fatty acids and certain amino acids burn to acetic acid directly. Actually, whatever fuels do not become pyruvic acid do become acetic acid. For all fuels, regardless of their original character, eventually transform to C₂, and all C₂ fragments finally become C₁ fragments in exactly the same way.

The transformation of acetic acid to CO₂ occurs through a *cycle* of reactions. Acetic acid is funneled in at one point of the cycle, its two carbons emerge at other points as CO₂, and the starting condition is eventually regenerated. The whole sequence is known as the citric acid cycle, a name taken from one of the substances which form the "endless belt" of the cycle.

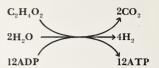
The energy harvested in this cycle is far greater than that gained in all previous reactions together. Per molecule of acetic acid, about one dozen new ATP molecules arise, partly through fuel oxidations, partly through H transfer to oxygen. Hence the citric acid cycle is the most important phase of fuel breakdown as a whole.

We may depict this cycle as in Fig. 13.10. This figure shows that acetic acid first combines with a C_4 molecule normally present in cells and six-carbon *citric acid* is thereby formed. This acid subsequently loses two carbons, one at a time, and so regenerates the C_4 starting condition. In addition to acetic acid, the only other raw material is $2H_2O$. The products are $2CO_2$, $4H_2$ (which are transferred

FIG. 13.10. Abbreviated summary of the citric acid cycle.



to oxygen), and a total energy gain of 12ATP (which includes the energy obtained through H transfer). In summary,



The general result

With the complete conversion of fuel to CO₂, combustion has reached its endpoint. What is the overall tally? Suppose we choose glucose as the starting fuel and trace the fate of its carbons, hydrogens, and oxygens.

As we have seen, the net conversion of one molecule of free glucose to pyruvic acid is described by the equation

$$C_6H_{12}O_6 \rightarrow 2C_3H_4O_3 + 2H_2$$

Four ATP is obtained from glucose breakdown as such. It can be shown also that each H₂ transferred via carriers to oxygen yields 3ATP. Hence the transfer of the 2H₂ above will yield 6ATP. Thus the total aerobic energy gain up to the pyruvic acid stage is 10 ATP.

Next, two pyruvic acid molecules are transformed into acetic acid, according to the equation

$$2C_3H_4O_3 + 2H_2O \rightarrow 2C_2H_4O_2 + 2H_2 + 2CO_2$$

The energy yield here is 2ATP from fuel oxidation, plus, again, 6ATP from the transport of $2H_2$ to oxygen. The total is 8ATP.

Finally, in two turns of the citric acid cycle, one for each of the two acetic acid molecules,

$$2C_2H_4O_2 + 4H_2O \rightarrow 8H_2 + 4CO_2$$

Here the net energy yield from both fuel oxidation and hydrogen transport is 12ATP per turn of the cycle, or 24ATP for two turns.

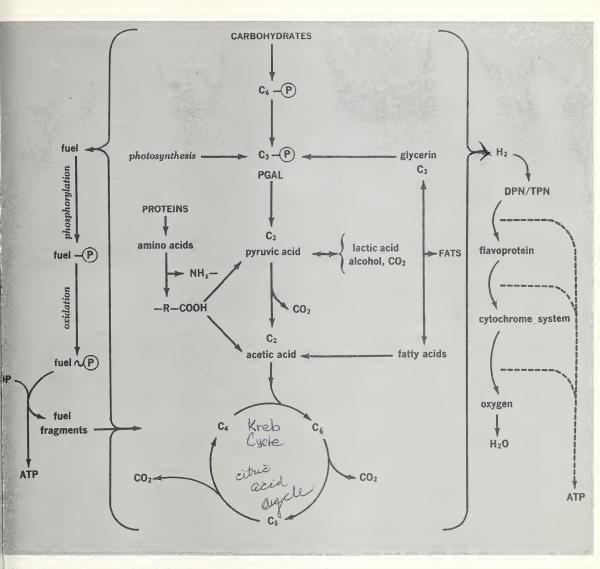
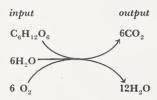


FIG. 13.11. Overall summary of respiration. The center panel outlines the main pathways of the respiratory breakdown of carbohydrates, fats, and proteins. Note here that all reactions shown are reversible and that if they are read in reverse, they indicate pathways of synthesis. The left-hand panel summarizes the general nature of any of the respiratory reaction sequences which occur in the center panel, and the right-hand panel, similarly, summarizes the process of hydrogen transport. The two sources of ATP gain are indicated also.

If we now add the three equations above, we obtain

$$C_6H_{12}O_6 + 6H_2O \rightarrow 6CO_2 + 12H_2$$

The 12H₂ has been transferred to atmospheric oxygen, yielding water. Twelve oxygen atoms, or 6 O₂, are required to accept 12H₂, and 12H₂O then forms. Hence we have, overall,



Moreover, the *major* endproduct is an energy yield of 42 molecules of ATP gross, for each molecule of glucose burned aerobically. This contrasts sharply with the gross yield of only 4ATP when glucose is burned anaerobically.

If a fuel other than glucose is used, different quantities of oxygen are likely to be required and different amounts of CO₂, water, and ATP will be produced. Whatever the fuel, more ATP is always

gained than is expended in phosphorylations, and it is this net gain which makes the long reaction sequences of vital adaptive value. The entire pattern of respiration is outlined in Fig. 13.11.

In cells, these metabolic processes take place exceedingly fast. For example, a glucose molecule is estimated to be burned completely within a single second. Considering the number of reactions, reactants, enzymes, carriers, and the like, such speed is truly impressive. In mammals, moreover, respiratory rates are greatly influenced by the thyroid hormone thyroxin. This hormone accelerates respiration in proportion to its concentration. How this effect is achieved and what particular reactions are influenced is still more or less completely unknown. Most organisms are not mammals, and their respiration is not under thyroxin control. Nevertheless, respiratory breakdowns still occur extremely rapidly. Very efficient enzyme action provides part of the answer. The remaining part of the answer undoubtedly lies in the close, ordered proximity of all required ingredients in the submicroscopic recesses of the mitochondria. Just as a well-arranged industrial assembly line turns out products at a great rate, so do the even better arranged mitochondria.

The fate and function of their chief product, ATP, is our next subject.

REVIEW QUESTIONS

- 1. Contrast a fire with respiration. What is common? What is different? Which materials are fuels in respiration? What three general types of events occur in respiration?
- 2. What is oxidation? What happens to the atomic pattern of a molecule during oxidation? What is the result of oxidation in terms of bond energies?
- 3. Describe the role of phosphates in respiration. What is the ADP-ATP system, and how does it function?
- 4. What is dehydrogenation? Where does it occur, and what role does it play in respiration? In what general way is hydrogen transferred to oxygen? Review the pattern of ATP formation during this transfer. To which specific carriers is hydrogen first transferred from fuel?
- 5. Distinguish between aerobic and anaerobic respiration. In which organisms, and under what conditions, does either occur? Review the specific sequence of carriers in (a) aerobic H transfer and (b) anaerobic H transfer. How and where may transfer in (a) become blocked, and what happens then? What endproducts are formed in (b), and what are the subsequent fates of these?
- 6. What is the general significance of pyruvic acid, acetic acid, and CO₂ in the respiratory breakdown of fuels? Review the chief steps in the breakdown of carbohydrates to pyruvic acid.
- 7. Which classes of foods break down to pyruvic acid during respiration, and which to acetic acid? Describe the steps of these breakdowns.

8. Review and summarize the overall fate of one molecule of glucose during complete respiratory combustion. What is the total net input here, and what is the total net output? What happens to the individual atoms of glucose? What is the total ATP gain, and how much

is gained during each of the main steps of breakdown?

9. Review the general and the specific interrelations of respiration and photosynthesis. Are the two processes in any sense the reverse of each other?

SUGGESTED COLLATERAL READINGS

Green, D. E.: Enzymes in Teams, Sci. American, vol. 181, 1949.

—: The Metabolism of Fats, Sci. American, vol. 190, 1954.

----: Biological Oxidation, Sci. American, vol. 199, 1958.

Levine, R., and M. S. Goldstein: The Action of Insulin, Sci. American, vol. 198, 1958.

Siekevitz, P.: Powerhouse of the Cell, Sci. American, vol. 197, 1957.

Stumpf, P. K.: ATP, Sci. American, vol. 188, 1953.
 Zamecnik, P. C.: The Microsome, Sci. American, vol. 198, 1958.

CHAPTER 14

Cellular metabolism: energy utilization

In what cellular processes must energy be expended? In all processes which contribute to the maintenance and self-perpetuation of a cell.

Such processes include physical as well as chemical ones. Probably the most important physical role of energy is to produce *movement*, of whole cells or their components. Subsidiary physical roles are the production of *heat*, of *light*, and of *electricity*. The chief chemical roles of energy are maintenance of respiration itself and, above all, maintenance of activities associated with the *synthesis* of new protoplasmic parts. Such parts must be manufactured to offset the combustion and the wear and tear of

existing ones, to make possible protoplasmic repairs after injury, to maintain growth, and to permit reproduction.

Under the heading of energy utilization, therefore, the two major subtopics are the physical uses and chemical uses of energy.

PHYSICAL USES OF ENERGY

Movement

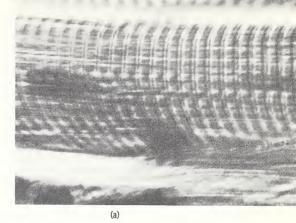
Probably the most abundant physical use of ATP is made in *mechanical* cell functions. And of these mechanical functions, production of **movement** is

undoubtedly the most widespread. Muscular movement in particular plays a vital role among animals (Fig. 14.1). It is the muscular system which maintains breathing, heartbeat, blood pressure, posture, and shape, even during "inactive" periods like sleep. Moreover, muscles are quantitatively the most conspicuous components of animals. For example, in an animal such as man, as much as one-third of the body is muscle. A proportionate amount of all available energy therefore must be expended to keep muscles contracting.

Muscle action in many ways resembles the stretching and releasing of a rubber band. Thus, when a rubber band is stretched, energy is supplied from the outside, and the stretched band then is rich in potential energy. When released, the band snaps together, and in this, the potential energy becomes actual and is spent in the mechanical work of contraction. Similarly in muscle. External energy must first be put into a muscle to extend it, and this energy is spent subsequently during contraction (Fig. 14.2).

The energy donor in muscle is ATP. To extend and so "charge" a muscle, respiratory ATP must be put into it. A muscle cell then stays in this energized condition until a nerve impulse arrives. Such an impulse is the trigger which brings about the "discharge" of the muscle; i.e., the impulse corresponds to releasing a stretched rubber band. As the muscle cell now contracts, its energy is spent in the contraction and ATP converts to ADP in the process. New ATP must then be put in to recharge the muscle once more (Fig. 14.3).

The details of these events are still far from being fully understood, but the basic process has been demonstrated in dramatic experiments. With appropriate procedures, proteins may be extracted from muscle tissue and fashioned into artificial fibers. These protein fibers may be put into a water bath, and some ATP may then be added. When this is done, it is found that as soon as ATP reaches one of the protein fibers, the fiber contracts violently! Indeed, such a fiber may lift up to 1,000 times its own weight, just as a living muscle may do. And it



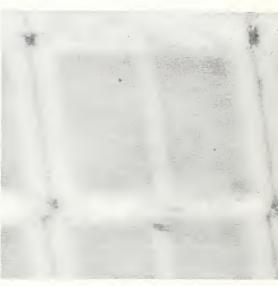


FIG. 14.1. The structure of a skeletal muscle. A whole muscle fiber is shown in (a). Note here the cross-striations, the internal longitudinal myofibrils which house the contraction apparatus, and the many nuclei, which appear as dark patches. (b) An electron micrograph of a few individual myofibrils. Note that each myofibril in turn consists of bundles of still finer fibrils. These latter are the functional units of the contraction machinery. Note again the prominent cross-striations. ((a) General Biological Supply House, Inc.; (b) courtesy of Dr. K. R. Porter, Rockefeller Institute.)

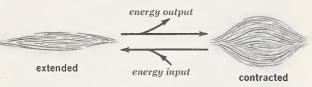


FIG. 14.2. The basic contraction-extension cycle of muscle action.

is also found that in a contracted fiber, ATP is no longer present but ADP is present instead. Such experiments suggest that the protein of a living muscle probably represents a major component of the contraction machinery and that ATP does indeed play a basic role in contraction.

Muscular motion is not the only form of movement among living systems. As we have seen in earlier chapters, flagellary, ciliary, and ameboid movements are widespread too. In all these, ATP again appears to be the common energy source. But the action cycles here are understood even less well than those of muscular contraction. Some evidence suggests that the beat of cilia and of flagella is produced by alternate contraction and relaxation of ultrafine protein filaments. If so, a machinery essentially like that of muscle may conceivably be involved. Contractile protein fibrils energized by ATP also may play a role in the movements of chromosomes during cell division (Chap. 19).

But the energizing of mechanical cell functions is not the only physical role of ATP. Production of heat, of light, and of electricity is an additional household task of many a cell type, and ATP is the energy donor here too.

Heat production

Cellular heat has a number of sources (Fig. 14.4). One source is the external environment, which supplies heat in varying amounts. Another source is the heat generated within cells by the friction of moving parts. And a third and major source is ATP. For when ATP is used within cells, it is hardly ever used with 100 per cent efficiency. When ATP produces movement, for example, a certain fraction of the energy of ATP escapes without doing useful mechanical work. This escaping energy dissipates in the cell in the form of heat. Also, when ATP phosphorylates a fuel in respiration, ATP loses a high-energy $\sim \mathbb{P}$ group, but the fuel only gains a low-energy $-\mathbb{P}$ group. The energy difference between $\sim \mathbb{P}$ and $-\mathbb{P}$ again dissipates in the form of heat.

Within organisms, heat maintains body temperature and offsets heat lost to the environment by evaporation and radiation; creates tiny convection currents within cells, and so assists in diffusion and osmosis in and among cells; and provides adequate operating temperatures for enzymes and all other functional parts of cells. Heat production in birds and mammals is balanced dynamically against heat

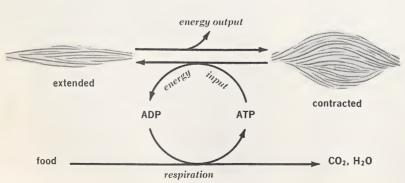
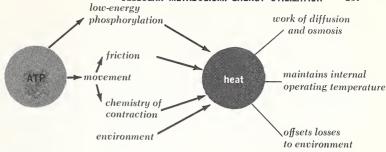


FIG. 14.3. The energy relations in muscle action. Food, via respiration, supplies energy for muscle contraction. Read the diagram from the bottom up.

FIG. 14.4. The principal sources and functions of heat in organisms.



loss, and a constant protoplasmic temperature is thereby maintained. But constant or not, heat is an essential requirement of every acting system, and if ATP served no other function than heat production, it would still be among the most vitally necessary components of protoplasm.

Bioluminescence

Living light is emitted by virtually all major groups of organisms. Bacteria, fungi, algae, and practically all animal phyla include marine or terrestrial representatives which are bioluminescent. Evidently, the capacity to produce light has developed several times independently during evolution. Yet the essentials of the light-generating mechanism appear to be alike in all cases. The main parts of this mechanism are a series of proteins, some of them enzymes, found in the cells of specialized *light-producing organs*. When oxygen and ATP are added to these proteins, a flash of light is produced. If more O₂ and ATP are added, a new flash is generated. That this is so can be shown by experiments with extracts of bioluminescent organs.

Bioluminescent bacteria and fungi may stay lit up continuously, but most animal light producers flash discontinuously (Fig. 14.5). The emission of a flash here depends on nervous stimulation of the light-producing organs. The light emitted by different organisms may be of any wavelength in the visible spectrum; that is, to the human eye it may be red, yellow, green, or blue.

Some organism may light up in several colors at

once. In all cases of bioluminescence, the energy of ATP is spent very efficiently, for little heat is lost during light production. Hence the frequent designation of living light as "cold" light. Also, the unit intensity of the light is remarkably great. It compares favorably with that of modern fluorescent lamps.

Bioelectricity

Bioelectricity is a byproduct of all protoplasmic processes in which ions play a part. In other words, electricity is as common throughout the living world as table salt. However, certain eels and rays are highly specialized in their capacity to produce electricity. These fish possess *electric organs*, com-

FIG. 14.5. Test-tube culture of bioluminescent bacteria. The continuous light they emit is strong enough to illuminate a portion of a printed page. (Carolina Biological Supply Co.)



posed mainly of modified muscles. They function somewhat like storage batteries connected in series.

The details of operation here are understood less well than those of light production. But it is quite clear that ATP again is the energy source. As in light production, the efficiency of energy utilization is remarkably great. So also is the intensity of the electricity generated. An electric eel may deliver a shock of up to 400 volts, enough to kill another fish, or to jolt a man severely, or to light up a row of electric bulbs wired to a tank into which such an eel is put. Nervous stimulation of the electric organ triggers the production of electricity.

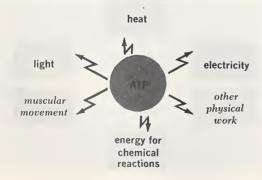
It is still unknown just how the chemical energy of ATP is actually converted into light energy or electrical energy. But that ATP is the key is clearly established, and this versatile compound emerges as the source of all forms of living physical energy, usual or unusual. Indeed, ATP is even more versatile, for it is also the source of all living *chemical* energy (Fig. 14.6).

CHEMICAL USES OF ENERGY

Synthesis patterns

Breakdown of organic compounds leads to a net build-up of ATP through respiration. Conversely, breakdown of ATP leads either to physical activity as discussed above or to a net build-up of organic

FIG. 14.6. General summary of the functions of ATP.



compounds through chemical synthesis. Figure 14.7 outlines this basic balance of energy and materials, which governs the overall metabolism of all cells.

Synthesis of protoplasm and breakdown occur simultaneously, all the time. As already noted in the last chapter, breakdown may affect any protoplasmic constituent regardless of composition or age. A protein just synthesized through long reaction sequences, and at great expense of energy, is just as likely to be destroyed as a glucose molecule already present for days. A certain *percentage* of all cellular constituents is decomposed every second, and which constituents actually make up this percentage is largely a matter of chance.

Such randomness applies also to synthesis. Regardless of the source of materials, a certain percentage of available molecular components is synthesized every second into finished protoplasm. If synthesis and breakdown are exactly balanced, the net character of a cell may remain unchanged. But continuous turnover of energy and materials occurs nevertheless, and every brick in the building is sooner or later replaced by a new one. Thus the house always remains "fresh."

Synthesis and breakdown cannot sustain each other in a self-contained, self-sufficient cycle, even when the two processes are exactly balanced. For energy dissipates irretrievably, through physical activities and through heat losses in chemical reactions. And materials dissipate through elimination, evaporation, and friction. Just to maintain a steady state, therefore, a cell must be supplied continuously with energy and raw materials: solar energy, CO₂, and water in the case of photosynthesizing cells, and in the case of all other cells, condensed packages of these three, namely, organic nutrients. Very often, moreover, the rate of supply of such materials must exceed the rate required for mere maintenance, for net synthesis may exceed net breakdown: in growth, in repair after injury, and in many specialized secreting cells, which manufacture materials for export to other cells.

With certain important exceptions, synthesis reactions generally are the exact reverse of breakdown

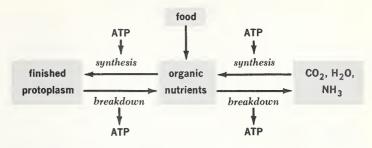


FIG. 14.7. The fundamental metabolic balance of cellular energy and materials.

reactions. Almost invariably, they require ATP rather than yield it. And whereas energy-yielding respiration revolves largely around carbohydrates and fats, protoplasm-yielding synthesis revolves largely around proteins and fats.

Protein synthesis

Protein synthesis is the key to cellular maintenance and self-perpetuation, for proteins are the most important organic components of cell structure and cell function. Not only do they make up the skeleton of the protoplasmic framework, but they also serve as enzymes and, in the form of nucleoproteins, as the fundamental regulators of cellular characteristics. The very nature of a cell depends largely on its proteins, and the kinds of proteins a cell contains are themselves traits regulated by proteins, namely, nucleoproteins.

What sets protein synthesis apart from most other syntheses is the condition of specificity, already referred to in Chap. 6. Proteins are made up of 23 different kinds of amino acids, and each protein contains a given number of each of these acids, arranged in a very particular sequence. This is what accounts for the differences among proteins; i.e., this is what makes proteins specific. The situation is not so with most other compounds. Glycogen, for example, is more or less always the same, no matter where or when it is found. For glycogen consists of a dozen or so glucose units, and since all glucose units are identical, it does not matter in what sequence the dozen are joined. Hence glycogen is

nonspecific. But the proteins, and especially the nucleoproteins, of any two cell types or organisms are never identical.

Therefore, *more* is needed for the synthesis of a protein than for the synthesis of any other type of compound. To synthesize a glycogen molecule, for example, all the cell needs is enough glucose units, energy, and enzymes capable of joining these glucose units together. To make a protein, however, the cell needs more than amino acids, energy, and appropriate enzymes. For although the enzymes can combine the amino acids, they cannot regulate the proper *sequence*, the pattern, in which the acids must be joined. Hence, if a cell is to synthesize specific proteins, it requires an agent which controls the pattern of amino acid combinations.

The ultimate guardians of protein patterns in a cell are nucleoproteins, in particular the genes, carriers of hereditary characteristics. We shall see in Chap. 16 how these vital nucleoproteins function. Here we shall simply take their specificity-controlling role for granted (Fig. 14.8). Note that protein breakdown, like the breakdown of any other compound, can occur without immediate participation of genes. For the precise pattern of breakdown is relatively unimportant so long as breakdown is accomplished in some way. Pattern becomes important only in building. That is why protein synthesis is not necessarily the reverse of protein breakdown. And that is also why the synthesis of most other protoplasmic components is essentially the reverse of their breakdown and does not require direct gene

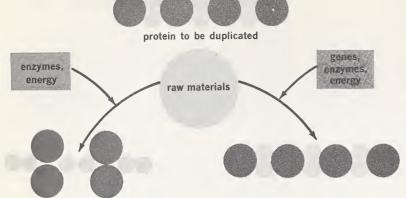


FIG. 14.8. The requirement of specificity control in protein synthesis. Without gene control, the structural pattern of new proteins would not match the pattern of pre-existing proteins.

new protein does not match original: gene control absent

new protein does match original: gene control present

action. For no matter in what sequence an enzyme links 12 glucose molecules together, the result will be the same glycogen.

All proteins existing on earth trace back to amino acids manufactured by plants. Out of hundreds of theoretical possibilities, plants produce just 23 different kinds of amino acids. Why only 23? Why these particular 23? The answers are unknown. If the first living system on earth had contained other amino acids, life today might be radically different from what it is.

We recall that the general structure of an amino acid is NH₂-R-COOH. Plant cells manufacture the amino part (NH2-) from nitrate ions which are absorbed as mineral nutrients. The -R-COOH parts are prepared from carbohydrate or fatty starting materials. Once produced, NH2- and -R-COOH may be combined into amino acids. Animal cells may make such combinations also. But they can manufacture neither the NH₂groups nor 8 to 10 of the 23 different kinds of -R-COOH groups. These 8 or 10 "essential" -R-COOH groups must enter animal food chains from plants, in prefabricated form. The 13 or 15 "nonessential" -R-COOH groups may be constructed in animals as in plants, from carbohydrate and fatty starting materials (Fig. 14.9).

Given 23 varieties of amino acids, every cell—but no biochemist as yet—is capable of synthesizing proteins. This function is performed largely, if not exclusively, in the microsomes, extremely fine granules dispersed abundantly throughout the cytoplasm of a cell (Chap. 6). Again we find an important biochemical activity being carried out in specialized "factory" locations. The microsomes contain all the necessary chemical equipment for protein synthesis, including, as we shall see, the crucial specificity-controlling agents.

Disregarding this problem of specificity control for the time being, the chaining together of amino acids is the reverse of protein digestion. Whole proteins are digested to individual amino acids by progressive *hydrolysis*, that is, addition of water (Chap. 11), and amino acids become whole proteins by progressive *dehydration*, or removal of water. Such removal of water links amino acids together, in much the same way that removal of water links glucose units together in the synthesis of polysaccharide (Chap. 10). The enzymes within cells which accomplish the joining of amino acids are called cathepsins (Fig. 14.10).

Protein synthesis appears to be an "all-or-none" phenomenon. It can take place only if all required amino acids are available in a cell simultaneously.

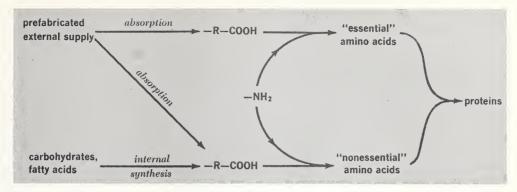


FIG. 14.9. In animals, the so-called "essential" amino acids cannot be synthesized and must be supplied prefabricated from the outside. Nonessential amino acids can be synthesized internally. Both kinds are required in the synthesis of proteins. Autotrophic organisms are capable of making all amino acids by internal synthesis, and here all amino acids therefore are "nonessential."

If the acids arrive a few at a time, construction cannot proceed part way and later continue to completion. This is probably correlated with the structural complexity of the compounds formed. If the building blocks were all alike, stepwise synthesis might be possible, since the blocks could be used interchangeably. But the building blocks are not alike, and as everyone knows, a single missing screw of a particular type may well prevent the assembly of a complex machine.

Finished proteins add to, or replace parts of, cellular components. For example, by virtue of its particular specificity, a protein may become incor-

porated into fibrils, membranes, mitochondria, chloroplasts, or indeed any other cellular structure. Alternatively, the properties of a newly formed protein might be such that it may come to function as a particular enzyme, or as a raw material in the synthesis of protein-containing complexes, e.g., nucleoproteins, hemoglobin, certain hormones, and many other vital compounds.

Other syntheses

The synthesis of polysaccharides and fats has already been discussed. For if the arrows are reversed, the respiratory reactions outlined in the preceding

H N
$$\sim$$
 R \sim CO OH $+$ N \sim R \sim COOH $\frac{cathepsins}{}$

FIG. 14.10. With the aid of cathepsins, which are proteinases, amino acids are joined in cells as shown. Two joined amino acids are a dipeptide, and the —CO—NH— bond which links them is known as the peptide link. Proteins are made by the stepwise joining together of amino acids through peptide links.

$$+ H_{2}O + N - R - CO - NH - R - COOH$$
H peptide bond

chapter describe such syntheses adequately (Fig. 13.11). Like proteins, fats and carbohydrates too become part of the structural and functional makeup of cells. In addition, they also serve importantly as storage materials and, together with proteins, as source materials for the construction of the innumerable other compounds of protoplasm.

A cell actually contains comparatively few proteins, carbohydrates, and fats as such. For most protoplasmic chemicals are direct or indirect derivatives of these three categories of substances. The manufacture of such derivatives occurs largely through special reaction sequences, and the details in most cases still require experimental analysis.

But although the synthetic processes are poorly known, the products are known fairly well. Some of these products occur in all cells, and we have encountered a few of them in foregoing chapters: ADP, DPN, cytochrome, and others. Some syntheses are restricted to specific, variously specialized cell types. A good example of this is the production of chlorophyll, and of pigments in general, in particular cell types only. Characteristic synthesis products of certain tissues, plant tissues especially, have often proved to be useful to man—rubber, quinine, caffeine, nicotine, to mention only a few. It is still largely unknown what functions, if any, such substances might have in the very cells in which they are manufactured. Since such compounds are not

formed universally in all cells, they cannot be of general significance in metabolism. In some cases at least, they probably represent unique waste products, retained in the cells of organisms which do not possess specialized excretory systems.

Many syntheses benefit not primarily the cells in which they occur, but other cells or body parts to which the products are exported. These are secretion syntheses, important both in plant and animal maintenance (Fig. 14.11). Every cell is a secreting cell to some extent, for, at the very least, it exports metabolic wastes. But many cells in addition manufacture specialized secretions, and these may have a variety of roles. For example, they may be nutritive (e.g., glucose secreted by photosynthesizing cells), digestive (e.g., enzymes poured into the gut), excretory (e.g., urea secretion by liver), regulative (e.g., hormones secreted by given plant and animal cells), supportive (e.g., secretion of cellulose in plants, bone substance in animals), reproductive (e.g., aromatic attracting scents secreted by plants and animals), or variously protective (e.g., secretion of irritants and poisons by plants and animals, including the secretions of antibiotics by soil organisms). Indeed, there are few plant or animal functions that do not require secretions of some sort.

Secreting cells in animals are generally more highly specialized than in plants. They are **gland** cells, and often they are aggregated into distinct

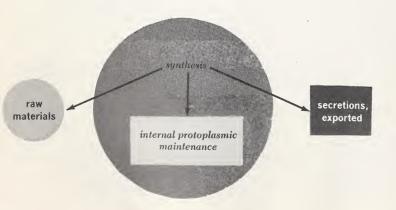


FIG. 14.11. The difference between maintenance synthesis and secretion synthesis in cells.

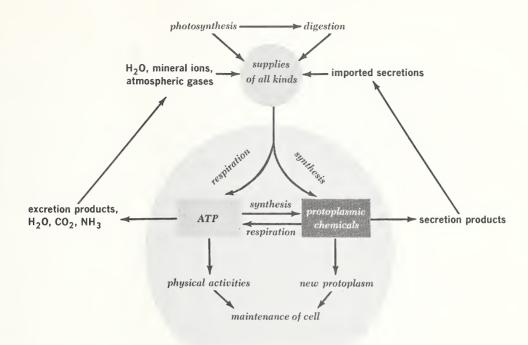


FIG. 14.12. The overall pattern of metabolism and its chief component processes.

glandular tissues or organs. The so-called exocrine glands empty their products into a free space or a duct. And the ductless endocrine glands secrete into the blood. Animal hormones are the products of endocrine glands. All other animal secretions are manufactured in exocrine glands.

Added to materials synthesized and used within a given cell, secretions received from other cells complete the ingredients required for the manufacture of cellular protoplasm. This multitude of chemicals, built up at the expense of ATP, then maintains and perpetuates the body of a cell (Fig. 14.12).

But it must not be imagined that newly constructed compounds just happen to arrange themselves into new protoplasm. If the proteins, fats, and other components were merely mixed together in water, the result would be a complex but lifeless soup. New protoplasmic constituents become "protoplasm" only if older protoplasm provides the framework. The house may be added to and its parts may be replaced or modified, but an altogether new house cannot be built. That apparently occurred only once during the entire history of the earth.

REVIEW QUESTIONS

- 1. In what respects are the contractions of a muscle and of a piece of rubber alike? What are the roles of ATP in muscle? In what specific ways is the ATP supply maintained? Describe the energetic aspects of a unit cycle of muscle activity.
- 2. Describe the ways in which organisms produce heat, light, and electricity. What are the properties of bioluminescence and bioelectricity, as compared with non-living forms of these energies?
- 3. Describe the basic balance of synthesis and breakdown in living organisms. How does protein specificity influence the ingredients required for protein synthesis? What are the ingredients? By what general sequence of

- processes, and also where, does protein synthesis occur?
- 4. Describe the specific sequence of reactions through which acetic acid in cells could be synthesized into (a) fats and (b) glycogen or starch. If necessary, consult Chap. 13.
- 5. What are the various possible functions of proteins, fats, and carbohydrates synthesized in cells? What are secretion syntheses? What is a gland, and what different kinds are there?
- 6. Review and summarize the broad components of metabolism as a whole, and review again the general relation between metabolism and self-perpetuation.

SUGGESTED COLLATERAL READINGS

- Harvey, E. N.: The Luminescence of Living Things, Sci.
 American, vol. 179, 1948.
- : Luminescent Organisms, Am. Scientist, vol. 40, 1952.
- Hayashi, T., and G. A. W. Boehm: Artificial Muscle, Sci. American, vol. 187, 1952.
- Johnson, F. H.: Heat and Life, Sci. American, vol. 180, 1949.
- Katchalsky, A., and S. Lifson: Muscle as a Machine, Sci. American, vol. 190, 1954.
- Szent-Gyorgyi, A.: Muscle Research, Sci. American, vol. 180, 1949.

Part Four

SELF-PERPETUATION: THE STEADY STATE

Metabolism is one-half of life; self-perpetuation is the other. The system which only metabolizes is but an inanimate machine, and an uncoordinated machine at that. To ensure internal coordination, to allow it to meet the impact of the external environment, and therefore to make it a living system, it must perform the processes of self-perpetuation. These make orderly metabolism possible—but they are themselves made possible by this metabolism.

We recall that self-perpetuation comprises three groups of processes: first, those which maintain the **steady state** of protoplasmic units and adjust and coordinate their internal operations; second, processes of **reproduction**, which extend the operations of protoplasmic units in space and in time; and third, processes of **adaptation**, which mold and fit the long-term character of protoplasmic units to the character of specific environments. Through self-perpetuation, living matter in the global aggregate becomes potentially indestructible.

Adaptation depends on reproduction, and reproduction depends on steady-state control. All three components of self-perpetuation operate on all levels of the living organization, and cellular self-perpetuation is prerequisite for the persistence of all higher levels. Consequently, maintenance of steady states within cells becomes the foundation of self-perpetuation as a whole.

Our plan of procedure for this first series of chapters is therefore clear. We begin with a discussion of the broad patterns of steady-state maintenance and examine here the principles of control and the kinds of controls encountered on various levels of protoplasmic organization. We then concentrate specifically on cellular steady states. In that context we inquire into the role of genes, which are the most important controlling agents, and into the roles of other cellular controllers, such as vitamins and hormones. Lastly, we deal with organismic steady states, i.e., controls on higher levels or organization. Here we concern ourselves particularly with the coordinating functions of blood, the excretory system, and the nervous system.

CHAPTER 15

The pattern of control

Any external or internal condition which tends to upset the normal, smooth operations of a system may be regarded as a stress. In a living system, external stresses are often produced by the environment: by enemies, injurious agents, lack of food, change of temperature, and innumerable other physical, chemical, and biological conditions. Internal stresses arise continuously as a result of the very operations of the system itself: fuels are used up, concentrations change, parts age and wear out, waste products accumulate, etc. In so far as any external or internal change, usual or unusual, affects living matter, any such change also becomes

a more or less significant stress. Actually, the living system is under stress all the time.

The problem of maintaining a steady state, therefore, is to counteract or to relieve stress. The requirement for this is, first, ability to recognize stress when and where it exists, and second, ability to react to such stress in self-preserving fashion. What is needed, in other words, is ability to recognize a stimulus and ability to carry out an appropriate response to that stimulus. So long as a system recognizes stimuli and reacts to them with fitting responses, it exercises control. And it may then remain intact and functioning, despite stresses

which would otherwise upset its internal coordination.

PRINCIPLES OF CONTROL

Components of control systems

In a system composed of many parts acting cooperatively, as in protoplasm, steady state will be preserved if the parts may continue to act in harmony despite stress. If a stimulus should change the action of one part, then, in response, the action of all other parts should change too, in such a way that the total action of the system still remains integrated and coordinated.

To achieve such persisting internal coordination, a first fundamental requirement is continuous and rapid flow of information among the parts of the system. Each part must be kept informed of what other parts are doing so that, if a stimulus affects one part, other parts may receive notice of it. Moreover, if the system is capable of responding to a stimulus in more than one way, a second fundamental requirement is ability to make selections. A simple system designed always to give the same response is not required to select. But where several

response possibilities exist, ability to decide among them clearly is crucial. For choice of inappropriate responses leads to *un*steady, not steady, states (Fig. 15.1).

Thus "control" ultimately becomes a matter of information and of selection. These terms imply messages or signals of some sort, message carriers, senders, receivers, transmission pathways, relays, switches, channel selectors—in short, all the components of a communications system. Indeed, in one form or another, communications systems are found wherever steady states are maintained. In protoplasm, we find them within cells and between cells, within organisms and between organisms, on all levels of organization.

All such protoplasmic communications operate on a common pattern. An initial stimulus irritates, or excites, a receiving device, called a receptor. Excitation of this receptor causes the emission of a signal, which is transmitted over a sensory pathway to an interpreting and response-selecting device, the modulator. This component sends out an appropriately chosen command signal, over an appropriately chosen motor pathway. The signal leads to an effector, a device which executes the commands.

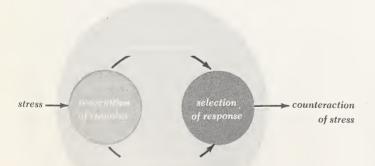


FIG. 15.1. The general pattern of maintenance and control of steady state.

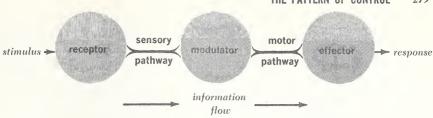


FIG. 15.2. The pattern of the control components in protoplasm.

This is the response which counteracts the original stimulus (Fig. 15.2).

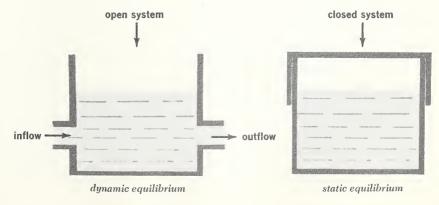
We may illustrate the operation of such a system by means of a mechanical model. Suppose that the water level of a flow tank, as in Fig. 15.3, is to be maintained in steady state; that is, despite possible variations of inflow or outflow (e.g., if an obstruction develops in one of the pipes, or if someone resets the speed of inflow or outflow), the water level is to stay at a predetermined height. Such a system is an open system, since materials are continuously entering and leaving, and the problem is to maintain a dynamic equilibrium. In these respects the model corresponds closely to living

entities, which also are open systems maintained in dynamic balance. By contrast, in a closed system nothing enters or leaves and balance is a *static equilibrium* (Fig. 15.3).

To establish a dynamic equilibrium in our model, we must install an automatic control device. Without help from external agencies, such a mechanism ought to be able to "sense" any change in water flow, and by means of valves, it should so readjust the inflow and the outflow that the water level in the tank remains relatively constant.

We have equipped our tank with automatic controls in Fig. 15.4. An air-filled float R functions as receptor. Inasmuch as it moves up or down with the

FIG. 15.3. The difference between an open and a closed system. Continuous flow characterizes the open system, and if a balanced condition is attained the equilibrium is dynamic. Nothing enters or leaves the closed system, and if an equilibrium is attained it is static.



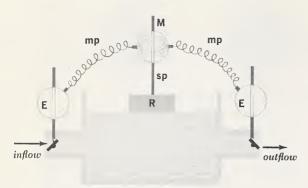


FIG. 15.4. Model of a steady-state maintaining device. R, receptor; M, modulator; E, effector; sp, sensory pathway, mp, motor pathway. If the system is adjusted as described in the text, then any change of inflow or outflow will bring about signals through $R \rightarrow sp \rightarrow M \rightarrow mp \rightarrow E$. Valve positions will then be adjusted in such a way that the change of inflow or outflow is counteracted and the original water level in the tank is reestablished.

water, it senses changes of water level. Any up or down motion of R is communicated via a rod sp, the sensory pathway, to the modulator M. Here the sensory message—up or down motion of sp—is interpreted, and appropriate commands for response are sent out. Imagine M to be a simple electrical trigger mechanism. It might be so built that any upward motion of sp trips a switch which makes an electric current of certain strength and duration flow through the wires mp. Similarly, any downward motion of sp would reverse the switch position, and another electrical impulse, of different strength and duration, would be produced. Indeed, possible switch positions might be more numerous, and each might cause the flow of a current of unique characteristics. These electrical impulses are the command signals, transmitted over the motor pathways mp to the two effectors E. The effectors are engines which operate the valves at the inflow and the outflow. They are so built that each different command signal received makes them move the valves into different positions.

Imagine now that for some external reason the inflow decreases. The outflow is still as before; hence the water level will begin to drop. But at once the modulator M will be informed of this change via R and sp. Appropriate electric signals will now go to the effectors, and the inflow valve will open more, the outflow valve close more. As a result, before the water level can drop very far, net inflow will increase and the water will rise back to normal. This new change of level will again be communicated to the modulator, new signals will go out to the effectors, and the valves will be returned to their original position.

If at this point the inflow is still reduced, the control device will go into action once more, precisely as above. Clearly, by readjusting as often as necessary, the device is capable of maintaining a steady state despite changes in the "environment."

Properties of control systems

Our model illustrates a number of features common to control systems, protoplasmic ones included.

First, internal operating energy is needed to make the system work. In the model, energy is required for the transmission of electric signals and for the motors which move the valves. In living control systems, similarly, small amounts of energy are needed for the transmission of information and comparatively large amounts of energy are required to operate the effectors. All these energy requirements are supplied by ATP.

Another common feature of control devices is that response to a stimulus is not a sudden, single event, but a stepwise, repeated one. In our model, a small initial change in valve position will produce a small initial change in water level. The receptor immediately signals to the modulator that a certain adjustment has been carried out. Accordingly, the modulator then cues the effectors to continue, to stop, or to reverse operations. The resulting effector action is essentially a new stimulus, which is again communicated back via the receptor to the modulator. Continuous information thus passes from sensory to motor component and from motor back

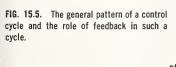
to sensory component. Many such cyclical passages of information, each contributing a small effector action, are usually required before a total response to a stimulus can be achieved. Indeed, the control device is not at rest even then. For in the absence of environmental stimuli, the receptor in effect signals "no change" to the modulator, the modulator sends "no adjustment required" to the effector, and the effector then informs the receptor of "no operation."

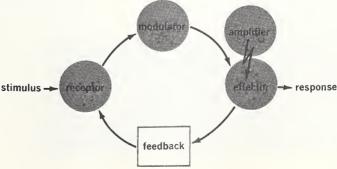
In such unceasing cyclical passages of information, we note that a response is "fed back" into the sensory end of the regulating device as a new stimulus, informing of the degree of counteraction already accomplished. The new stimulus in turn, fed into the modulator, informs of the degree of counteraction yet to be carried out. Feedback is to the motor-sensory segment of the cycle what modulation is to the sensory-motor segment. Both feedback and modulation control the direction, the amount, and the duration of adjustment. In protoplasm, as elsewhere, control activity becomes effective control only if appropriate feedbacks are operative. Without feedback, the modulator would never become aware of what the effector has been doing; hence it would never be able to send out "correct" new commands (Fig. 15.5).

Feedbacks and continuous cycles of information account for yet another common property of control

systems: they function essentially by trial and error, by "hunting" for the correct equilibrium condition. Refer again to the model in Fig. 15.4. Suppose that the inflow changes so as to cause an initial drop in water level. Depending on the sensitivity of the apparatus, a given number of seconds may elapse before the valves are brought into corrective positions. By that time, the water level may be down 1 in., say. Now the water begins to rise, but again there will be a time lag of some seconds before the effectors receive the new command to return the valves to normal. But by that time, the water may already have risen somewhat above the correct level. Fresh signals to reverse valve positions a bit will now be forthcoming, and by the time that action is executed, the water may be down again below the appropriate level.

Most controls overshoot in this fashion, and they undergo hunting oscillations to either side of the equilibrium state. Clearly, it will be important that such oscillations either become smaller and smaller till they subside or else continue at constant amplitude. Poorly adjusted control devices often produce ever-increasing hunting oscillations, in which case "steady" state, of course, will not be maintained. The zigzagging locomotion of a drunk walking toward a stated object is a familiar example of this. Under the influence of alcohol, nervous control over locomotion becomes loose and imprecise and





increased hunting oscillations occur. Normally, such oscillations are so small and they subside so rapidly that straight-line locomotion is possible.

Control mechanisms have inherent limits of efficiency. If they are overloaded, that is, if they must work too fast or too hard, they may become "neurotic." They may make errors in sensing stimuli, or in interpreting signals, or in selecting and executing responses. Extreme overloading may cause internal structural breakdowns, which may make the device inoperative altogether. In protoplasm, functional or structural failures of control systems result in *disease*. Disease itself is a stress stimulus to other, still intact regulating devices, and repair or circumvention of the diseased condition may ensue.

PROTOPLASMIC CONTROLS

The regulating devices of protoplasm are organized into a hierarchy, in accordance with the hierarchy of protoplasmic levels of organization. Cells contain complete internal control systems made up of molecules. Tissues contain control systems made up of cells. Organs contain control systems made up of tissues, etc. In such an order, the functioning of lower-level controls is essential for the functioning of any higher-level controls. Hence controls among protoplasmic molecules are the foundations of all protoplasmic control (Fig. 15.6).

Molecular control

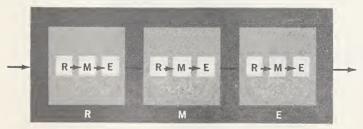
Regardless of how a cell is stressed, the stress stimulus usually affects one or more metabolic processes.

For example, changes in nutrient supplies, waste accumulation, injury, pH change, temperature change, sol-gel transformations, or indeed any other physical or chemical stimuli are likely to influence a cell either by accelerating or by decelerating particular metabolic reactions. Also, regardless of how a cell responds, the response is ultimately produced by metabolic processes. For whatever the effector action of a cell may be, acceleration or deceleration of respiration, or of chemical activities such as synthesis, or of physical activities such as movement is likely to be involved.

Steady-state maintenance in a cell therefore becomes largely a matter of controlling cellular metabolism. The duration, speed, and amount of every reaction must be suitably geared to the duration, speed, and amount of every other reaction. And to maintain such coordination, every accelerated reaction must eventually be decelerated back to normal and every decelerated reaction must be accelerated back to normal.

Actually, a metabolic reaction is itself the simplest and most basic kind of control system. Molecules function as receptors, modulators, and effectors, and the water in which a reaction takes place serves as sensory and motor pathway. For example, consider the reaction

When this reversible reaction is in chemical equilibrium, the reaction to the left occurs as fast as the reaction to the right. No net change occurs, and the



R or M or E

FIG. 15.6. The protoplasmic hierarchy of control systems. R, receptor; M, modulator; E, effector. The entire control apparatus of one level (within a rectangular box) is a component of the control apparatus on the next higher level.

system therefore is in steady state. The totality of glucose molecules in a cell, called a glucose pool, may now function as receptor. For example, if additional glucose arrives in the cell as food, this will be a stimulus "sensed" by the glucose pool as an increase in concentration. The reaction to the right will then outbalance that to the left, and more glycogen will be formed. The glycogen pool here is the effector, and the increase of glycogen concentration is the response. For as glycogen accumulates at the expense of glucose, the glucose pool decreases back to normal—and the original stimulus is thereby removed. The extra glycogen, in turn, may represent a new stimulus in the cell, initiating other reactions and new responses.

Note that the designations "receptor" and "effector" are not fixed. If a cell were to acquire additional glycogen rather than glucose, then the glycogen pool would be the receptor and the glucose pool the effector. Note further that, in either case, the function of the modulator is performed by the enzymes. It takes a specific enzyme to "interpret" a specific stimulus and to direct the specific response. Because it is specific for a particular reaction, an enzyme cannot interpret various different stimuli, but only one. And it cannot select among several possible responses, but must promote the same response every time.

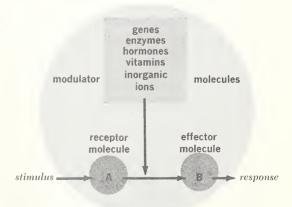
In addition to enzymes, four other kinds of reaction modulators occur in cells: vitamins, hormones, inorganic substances, and above all genes. These too control specific metabolic reactions. Indeed, practically all metabolic reactions appear to require enzymes plus various other agents. For example, we already know that the respiratory reaction which converts pyruvic acid to acetic acid requires vitamin B₁, the hormone thyroxin (in mammals), and it is also known to require magnesium ions. In general, most metabolic reactions require at least one enzyme, one or more vitamins, hormones, and inorganic materials as well. Moreover, there is now little doubt that every metabolic reaction depends ultimately on gene action.

All these categories of cellular modulators are

essentially enzymelike in their activities. Thus, like enzymes, genes, vitamins, hormones, and inorganic substances are specifically necessary for specific reactions; small quantities of them suffice; and they do not become part of the endproduct, but are recoverable intact and unchanged after the reaction. In short, they all function more or less like catalysts. And in the language of control systems, they function as information relays, or as modulators. They share with enzymes the property of being differentially sensitive to single sensory messages only and of promoting the same reaction responses every time, without freedom of choice (Fig. 15.7).

We may ask here why multiple controls for each reaction are required to begin with. Would not a single modulator suffice? Possibly it might, but there is safety in numbers. Multiple controls reduce the chance of error, and if one modulator becomes inoperative, the reaction may not be stopped completely. Multiple controls provide desirable redundancy, or repetition. If one wishes to make sure that information is received exactly as sent, then one repeats the message several times. Just so, chemical messages in metabolism are highly redundant, as are protoplasmic messages in general.

FIG. 15.7. The molecular modulators within cells.



Supramolecular control

All other protoplasmic controls are based on the molecular controls of metabolism. In the cell, molecules are variously aggregated into comparatively large formed structures, and these, by virtue of the control functions of their component molecules, carry out specific higher-level control functions of their own.

Many molecular aggregates within cells, visible under the microscope, serve as receptors. For example, pigmented granules absorb light and form excellent *photoreceptors*. Long filaments are sensitive to displacement, to pressure, to touch, and they may therefore serve as receptors of mechanical stimuli. Other formed microscopic structures may be sensitive to particular classes of chemicals, and they may function as *chemoreceptors*. Note that a cell does not necessarily possess receptors for all possible kinds of stimuli. For example, magnetic energy is generally not receivable as a stimulus.

Formed bodies also function as modulators. Of these, the cell nucleus is the most complex. Through its genes it ultimately controls all cytoplasmic activities. Complex modulators in the cytoplasm include, for example, the mitochondria, the microsomes, and the chloroplasts of plant cells. As we have seen in earlier chapters, these play vital specific roles in specific stimulus-response sequences.

Complex cellular effectors are equally varied. Many contribute to the numerous physical and chemical responses necessary in the *internal* maintenance of a cell. Others link a cell to its *external* environment. For example, some produce light, as in bioluminescent cells, or electricity, as in the cells of animal electric organs. Some bring about cell movement, and some absorb or secrete various substances through the cell surface.

A given cell part may have multiple control functions. It may serve as receptor in one instance, as modulator in another, as effector in yet a third. For example, the cell membrane is a receptor when it "recognizes" a glucose molecule, but it is an effector when it allows that molecule to pass

through. The cell nucleus has been reterred to above as a modulator, which indeed it often is. But it may also serve as receptor—it receives many stimuli from the cytoplasm; or it may be an effector—it executes many responses. Clearly, functional labels are not fixed.

The cellular level is the lowest on which we encounter modulators capable of distinguishing between various sensory messages and of selecting among various response possibilities. For example, the cell membrane is selectively permeable. Functioning as a modulator, it may interpret the chemical nature of different kinds of molecules in contact with it and it may "decide" how fast and to what extent each such molecule is to be passed through. Similar selectivity is displayed by other complex control components within a cell and also by all supracellular control systems.

How does this crucial capacity of making decisions arise? The answer is not yet clear. But note that a complex cellular modulator contains within it different *molecular* control systems, many of them, and each capable of a single response. It is therefore likely that the number of decisions a complex modulator may make is correlated with the number of different molecular unit systems of which it is composed.

Superimposed on the controls within cells, most animals (but not usually other organisms) possess regulating devices above the cellular level. Whole specialized tissues, organs, and organ systems serve here specifically as receptors, modulators, or effectors. As above, a given structure may function in more than one of these capacities.

A most important supracellular mechanism involves the blood as sensory and motor pathway. Change in any one part of the body is signaled to all other parts via the blood. A battery of modulators and effectors may be called into action as a result: heart, blood vessels, skin, kidneys, liver, endocrine and other glands, muscles, to mention a few. Their specific operation counteracts the original change. For example, see Fig. 15.8.

Probably the most familiar, and the most com-

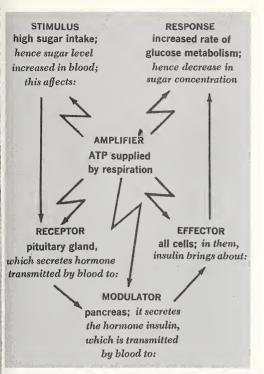


FIG. 15.8. An example of organismic steady-state control.

plex, control device is the nervous system. Sense organs, in the skin and within the body, are receptors. The brain is the chief modulator. Muscle-bone systems and glands function as effectors. Nerves serve as sensory and motor connecting paths. Transmission of information through such a sequence of

specialized neural structures, energized along its length by ATP, constitutes a *reflex*. An example is given in Fig. 15.9.

Reflexes are the basis of nervous steady-state control. They may, and often do, act in concert with other control mechanisms, for example, the hormone-producing endocrine system, the circulatory system, the digestive system, and many others. Most situations requiring control actually are regulated by a multiplicity of devices, and the nervous system often is one of them.

The general conclusion emerges that every part of protoplasm is controlled by all other parts and at the same time contributes to the control of all other parts. And since every structure, large or small, so functions in steady-state maintenance, "controlling" becomes a very major component of "living." Recognizing the stimuli of the environment, and actively responding to them, is just as characteristic of "being alive" as metabolizing. Indeed, control is the crux of self-perpetuation, and as we shall see, reproduction and adaptation are special forms of control. Without control, life becomes nonlife.

Conversely, nonlife became life when the first control mechanism came into existence. That, as we have seen, was the nucleoprotein molecule, the gene. All evolution ever since may be looked upon as a progressive development of more varied and more efficient control mechanisms. These were capable of counteracting more environmental stresses; hence they permitted the extension of life in each environment for longer periods. The controls developed in man are one culmination of this. Through exquisitely sensitive receptors, such as eyes and ears; through refined modulation, such as learning and

FIG. 15.9. A further example of organismic steady-state control. In this case, nervous reflexes are involved.

STIMULUS	RECEPTOR	MODULATOR	EFFECTOR	RESPONSE
approaching danger	eye; it signals	brain; it signals	muscles, bones;	running, and avoidance of danger

286

thinking; and through versatile responses, such as speaking, writing, and using tools for building and manufacturing, the human organism has become one of the best controlled, remarkably able to resist the stresses of the most varied environments.

This outlines the general pattern of protoplasmic control. We now refocus our attention on the individual cell and discuss the critical agents within the cell on which all self-perpetuation ultimately depends.

REVIEW QUESTIONS

- 1. In general terms, what kinds of processes take place in the execution of control activities? What general function do such controls serve in the maintenance of life? What is the role of information flow in the maintenance of steady states?
- 2. What are the structural components of every control system in protoplasm? What specific role does each such component play in the maintenance of dynamic equilibria?
- 3. Review the functional properties of control systems. What is feedback, and what is its significance in control activities?
- 4. What is the significance of trial and error in control activities? What happens when control systems are overloaded? Interpret the temperature-regulating action of a home thermostat in terms of a control system, and indicate the specific roles of feedback and trial and

- error. Do likewise for the temperature-regulating systems of mammals and birds.
- 5. Describe the hierarchical organization of the controls in protoplasm. How does interference with control at any level affect the controls of (a) lower and (b) higher levels?
- 6. In what sense does a molecular reaction constitute a control system? What kinds of substances may serve as molecular modulators? What functional characteristics do these have in common?
- 7. For each microscopic body usually present in cells, describe a cellular activity in which that body functions as (a) receptor, (b) modulator, (c) effector, and (d) sensory or motor pathway.
- 8. Review the pattern of protoplasmic control on supracellular levels. What is a reflex? Which plant or animal parts do *not* participate in control activities?

SUGGESTED COLLATERAL READINGS

- Brown, F. A.: Biological Clocks and the Fiddler Crab, Sci. American, vol. 190, 1954.
- Brown, G. S., and D. P. Campbell: Control Systems, Sci. American, vol. 187, 1952.
- Gerard, R. W.: The Dynamics of Inhibition, Sci. American, vol. 179, 1948.
- King, G.: What Is Information? Sci. American, vol. 187, 1952.
- Nagel, E.: Self-regulation, Sci. American, vol. 187, 1952. Tustin, A.: Feedback, Sci. American, vol. 187, 1952.

CHAPTER 16

Cellular controls

We have found in the preceding chapter that five categories of substances usually function as controlling agents within a cell: genes, enzymes, vitamins, hormones, and inorganic ions. About enzymes and ions much has already been said, and more will be said later. In this chapter, we concentrate on the remaining three categories, with particular emphasis on the most important of all, the genes.

GENES

Life began after the first nucleoproteins had been formed. Creation of this original life took billions

of years, for it had to occur by physical and chemical chance; there was no blueprint to follow. But after nucleoproteins appeared on the scene, creation of new life could become a very rapid process. Today it takes only 20 min to create a new bacterium, only 22 months to create a new elephant. This tremendous acceleration is made possible by nucleoproteins, more specifically by genes, the modern descendants of the first nucleoproteins. Present in every cell, genes do provide a blueprint, a recipe, not only for the creation of life, but also for its maintenance. Through genes creation and maintenance cease to be matters of chance but become matters of controlled planning.

Structure

We recall from Chap. 6 that the nucleus of a cell consists of an external membrane and a semifluid nuclear sap and that two kinds of structures are suspended in this sap: one or more spherical bodies,

FIG. 16.1. Chromosomes. In this stained preparation of insect chromosomes, characteristic cross-bands are clearly visible. Such banding is found in all chromosomes studied. (From D. F. Poulson and C. W. Metz, "J. Morphol.," Vol. 63, 1938.)



called **nucleoli**, and a number of elongated filamentous bodies, the gene-containing **chromosomes** (Fig. 16.1).

We recall also that the number of chromosomes per nucleus is an inherited trait, constant for each species. A fertilized egg of an organism possesses a given number of chromosomes, inherited from the parents, and all the cells which arise from this egg in the development of an adult inherit that same number of chromosomes. Human cells, for example, usually contain 46 chromosomes. In most organisms, the number is even at least at one stage of the life cycle, and in very many of these, it is even for a substantial part, or virtually the whole, of the life cycle. Thus, alternative conditions notwithstanding, a largely even, fixed number of chromosomes houses the genes.

No one has ever knowingly seen one gene. This is not primarily because it is too small, but primarily because it is not a uniquely definable object. We may say, in general, that a gene is a unit of length within a chromosome.

But at least three different, more or less equally acceptable definitions of "unit" are possible. A gene may be (1) that minimum part of a chromosome which controls a single metabolic reaction in a cell; or (2) that minimum part of a chromosome which, when it mutates, i.e., changes structurally in some permanent way, alters just one trait of a cell; or (3) that minimum part of a chromosome which, in the nucleus of a reproductive cell, can transfer, or "cross over," to a neighboring chromosome. The significance of the events here referred to will become clearer later. For the present we merely note that a "gene" may be defined either as a unit of biochemical action, or as a unit of mutation, or as a unit of crossing over.

And these units usually are not identical. Any one of the units may be shorter or longer than any other, and this itself may vary for different genes.

We conclude, therefore, that the term "gene" does not refer to any specific, fixed piece of a chromosome, but rather to an *operational concept*. Just as the unit of physical length varies according to whether we define it in inches or in centimeters or in ells, so does the chromosome unit vary according to the experimental methods we use to measure it. Henceforth, when we refer to a "gene" without further qualifications, we shall keep in mind that we are making a rather vague reference to *some* section of a chromosome.

However carefully we must qualify the definition of a gene, we need not qualify similarly in considering the chemical composition of a gene. The whole chromosome is an integrated unit, and for chemical analysis it does not matter too much just exactly where one gene ends and the next one begins.

Genes, like whole chromosomes, consist largely of nucleoproteins. And as outlined previously in Chaps. 2 and 6,

nucleoprotein = nucleic acid + protein

A considerable body of information now available shows fairly clearly that it is largely, or entirely, the nucleic acid component, not the protein component, which endows chromosomal nucleoprotein with the properties of genes. For example, it is possible to extract nucleoprotein from one kind of bacterium and to separate this extract into nucleic acid and protein. If then the nucleic acid is experimentally transferred into another kind of bacterium, this recipient acquires genetic traits of the donor. This is not the case when the protein fraction is similarly transferred (Fig. 16.2). The functioning of genes therefore must be explained primarily in terms of the structure of nucleic acids.

About this structure much has already been said in Chaps. 2 and 6. To recapitulate briefly,

nucleic acid = many nucleotides

 $nucleotide = \begin{cases} purine or \\ pyrimidine \end{cases} + sugar + phosphate$

We recall that the sugar of a nucleotide may be either ribose or the related desoxyribose, and we

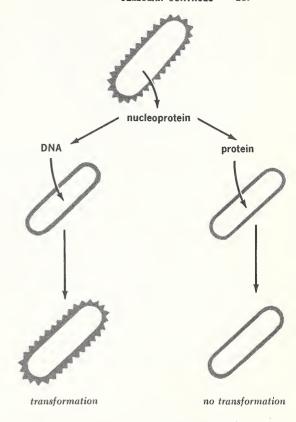


FIG. 16.2. Bacterial transformation. The nucleoprotein of a rough-coated bacterial type is extracted, and separate DNA and protein fractions are prepared. If a smooth-coated bacterial type is allowed to absorb the DNA fraction, it will change into a rough-coated type. But it will remain smooth-coated if it absorbs only the protein fraction. Experiments of this sort show that the nucleic acid part, not the protein part, of nucleoproteins is of genetic importance.

have noted this to be the basis of distinction between ribose nucleic acid, or RNA, and desoxyribose nucleic acid, or DNA. The nucleic acids of genes are invariably DNA.

In the many nucleotides of a DNA molecule, the

sugar is always desoxyribose. But the purines and pyrimidines are of four varieties. There are two kinds of purines, called adenine and guanine, and two kinds of pyrimidines, called thymine and cytosine. Accordingly, there are four varieties of nucleotides, namely:

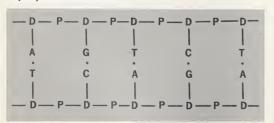
adenine-desoxyribose-phosphate guanine-desoxyribose-phosphate thymine-desoxyribose-phosphate cytosine-desoxyribose-phosphate.

Large numbers of each of these four are joined, in an unlimited number of sequences, to form a DNA chain.

Evidence indicates that DNA in genes actually is a double chain of nucleotides, one chain parallel to the other. The two chains are held together by their purines and pyrimidines, in such a way that a purine of one chain is attached to a pyrimidine of the other. More specifically, adenine is always joined to thymine, guanine to cytosine. Thus the structure of a double DNA chain in genes could be symbolized as in Fig. 16.3.

The figure indicates that four purine-pyrimidine pairings are possible, namely: —A·T—, —T·A—, —G·C—, and —C·G—. Apparently there is no limit to the number of times each of these pairings can

FIG. 16.3. The Watson-Crick model of DNA structure. P, phosphate; D, desoxyribose; A, T, G, C, purines and pyrimidines. A P-D-A unit represents one of the nucleotides. In this -P-D-D- double chain, four kinds of purine-pyrimidine pairs are possible, i.e., A·T, T·A, G·C, and C·G. Each of the four may occur very many times, and the sequence of the pairs may vary in unlimited fashion.



occur in a long double chain. Nor, apparently, are there restrictions as to their sequence. Thus the pairings may be regarded as an alphabet of four symbols, and "words" of any length may be constructed by using these symbols as often as desired and in any order. Evidently, the possible number of compositionally different DNA's is practically unlimited. This is reminiscent of the situation in proteins, where an alphabet of 23 amino acids gives rise to a virtually unlimited number of different complexes.

A final architectural characteristic of DNA is that its double chain is probably not straight, but spiraled (Fig. 16.4).

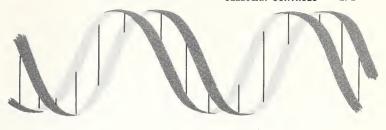
This concept of the structure of DNA is generally referred to as the Watson-Crick model, after the investigators who proposed it. It still leaves many problems unsolved. To cite just one, how and where is DNA joined to protein to form nucleoprotein? But the model does answer many other questions. For example, it explains the observed specificity of DNA. Just as proteins are specific by virtue of particular combination patterns among their amino acids, so, according to the Watson-Crick model, may DNA's be specific by virtue of particular combinations of their four-symbol alphabet. Such different DNA specificities undoubtedly account for the observation that although all genes contain DNA, genes are far from alike. Each organism contains sets of functionally different genes and the sets of one species differ from those of every other species.

Moreover, the Watson-Crick model may explain how genes might work.

Function

In previous chapters it has been stated repeatedly that genes ultimately control all activities of a cell. Research seems to indicate that genes perform this enormous job by, surprisingly, doing virtually nothing. As is characteristic of controlling agents generally, genes turn out to be, essentially, stable and more or less passive containers of information. The information in each case consists of a particular, specific sequence of purine-pyrimidine pairs. And

FIG. 16.4. A DNA double chain is spiraled as shown in this diagram. The two spirals symbolize the -P-D-P-D- chains, and the connections between the spirals represent the purine-pyrimidine pairs.



all that genes appear to do, or allow to be done to them, is to have their specific information *copied* by other kinds of information carriers. We are led to regard genes as serving rather like important original "text," carefully protected and preserved in the "library" of the nucleus. There they are available as permanent, authoritative master documents, from which expendable duplicates may be prepared.

The specific information contained within genes represents a set of building instructions, like the instructions given by a blueprint. These genetic instructions supply the chemical machinery of a cell with "orders" for just two kinds of building jobs: how to make new genes exactly like the originals, and how to join amino acids together to make specific proteins.

The first of these building activities occurs right inside the nucleus, every time a cell divides. Just before cell division, all the genes present in all the chromosomes are duplicated exactly; i.e., the chromosomes themselves duplicate. Two identical chromosome (and gene) sets are so produced, and one set is then incorporated into each of the two new cells formed by the division of the original cell. In other words, at the time of cell division, the original DNA molecules of the genes give instructions how to build two exactly identical sets of DNA molecules. This ensures that the specific genetic information of a cell is preserved and passed on unchanged to all succeeding cell generations.

The Watson-Crick model suggests how new DNA may be made from old. The process is believed to take place in three steps (Fig. 16.5). First, the purine-pyrimidine pairs which hold an original double

DNA chain together somehow become disengaged, and the double chain so "unzips" into two separate single chains. Second, each single chain now builds on to itself appropriate new nucleotides, present as raw materials. For example, every A (adenine) sticking out from the single chain may attach to itself a new T-D-P; or every C (cytosine) of the single chain may join to itself a new G-D-P. In this way, all the free purines and pyrimidines of the single chain may eventually combine with "right" nucleotides, drawn from the pool of nutrient raw materials. The third and final step then requires only a linking together of the newly attached nucleotides.

The overall result is that *one* original DNA double chain has given rise to two double chains. These are identical with each other as well as with the original double chain. DNA thus has reproduced, and specificity has been preserved exactly. Note that all DNA always incorporates the old and the new. One of its two nucleotide chains preexists; the other is newly manufactured.

This duplication process is as much a model as the Watson-Crick structure itself. To what extent it describes the actual process of gene duplication is quite unknown. But because it does show how gene duplication might occur, and because a better model is not available, it is widely accepted as a reasonable approximation of actual events.

The basic idea underlying this duplication model is often referred to as the template hypothesis. Each single nucleotide chain of DNA serves as a template, or blueprint, or master pattern, according to which a new, matching nucleotide chain is manu-

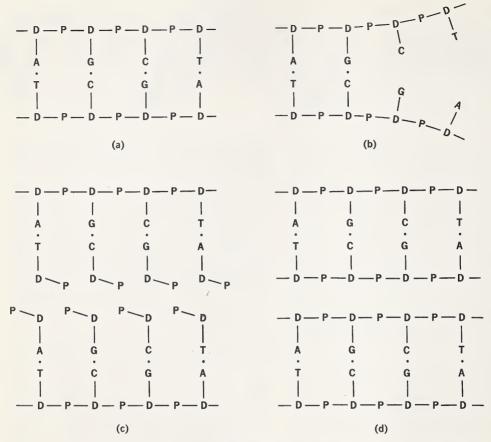


FIG. 16.5. Simplified representation of how DNA duplication may occur. (a) Initial stage. (b) The DNA double chain "unzips" into two single chains. (c) Each chain attaches appropriate new nucleotides to itself from the food supply. (d) Final pair of double chains.

factured. It is in this sense that genetic DNA may be regarded as passive, simply permitting its particular specificity to be copied and to be transferred to new DNA.

Granting that the specific information of DNA is preserved through successive cell generations, what is the functional value of this information in the life of a cell? As noted above, the value is that the genetic information instructs the cell how to build specific proteins. In this, a template principle is probably involved again. We already know that protein synthesis occurs in the cytoplasm, specifically in the granules called *microsomes*. But the genes which direct this synthesis are in the nucleus.

Hence there must be some kind of connecting link between genes and microsomes. Research has shown that this link is almost certainly *RNA*, the second kind of nucleic acid present in cells.

RNA occurs particularly in three places: in the chromosomes, in the nucleoli, and in the microsomes. And there is now ample evidence indicating that genes control protein synthesis in the following manner (Fig. 16.6). First, RNA appears to be manufactured in the chromosomes. In this process, the DNA of the genes probably serves as a template and the specific information of the different DNA molecules is copied and incorporated into the newly constructed RNA molecules. These RNA's therefore are specific, and they match the particular specificities of the DNA's. Second, variously specific RNA molecules then accumulate in the nucleoli, which may be envisaged as storage places for RNA. And third, specific RNA from the nucleoli eventually reaches the microsomes in the cytoplasm. Here the RNA molecules probably function as templates, or blueprints, in their own turn. For it is now believed that the particular sequence of the different purinepyrimidine pairings in RNA functions like a series of differently shaped "pigeonholes," each capable of holding an amino acid of particular chemical construction. When these amino acids are then linked together in the sequence imposed by RNA, the resulting protein will have a specificity which matches the specificity of RNA. And since that specificity has been determined by the genes, genes ultimately control the kinds of proteins a cell can synthesize.

Note here again that genes are passive. They allow only their specific information to be copied by RNA, which in turn allows that information to be used in protein manufacture. The advantage of this indirect functioning of genes is clear. Genes remain protected within the nucleus as in a vault and are therefore less subject to destruction by the respiratory metabolism of the cytoplasm. And when genetic information is required, genes do not move to the place of action themselves but send expendable copies of themselves in the form of nongenetic

RNA. In this sense genes may be likened to a policy-making board of directors, and RNA, to the foremen that actually execute the directives of the managing board.

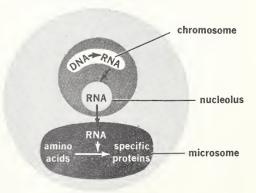
Consequences of gene function

By governing the synthesis of new genes and of specific proteins, genes play so strategic a role that they ultimately control the whole nature and the very life of every cell.

First, since proteins make up more of the formed solid framework of protoplasm than any other constituents, genes determine the basic architecture and structure of every cell. This means, too, that every normal architectural change during the life cycle of a cell and every architectural difference among the cells of one or of different organisms are ultimately gene-determined.

Second, by controlling the nature of proteins, genes control the nature of *enzymes*, all of which are proteins. Since practically every metabolic reaction in a cell requires at least one enzyme, genes so determine what kinds of **metabolic processes** are possible in a cell. Nutritional reactions, respiratory reactions, motion-producing reactions, synthesis re-

FIG. 16.6. The functional connection between DNA and RNA and the transport pathway of RNA from nucleus to cytoplasm.



actions of all kinds, all are enzyme-dependent, hence gene-dependent.

Third, by so governing the whole metabolic character of a cell, genes are the ultimate maintainers of steady state. For genes control not only themselves (by governing gene duplication), but also all other control agents within cells. Thus genes regulate the nature of enzymes, as already noted. Genes regulate hormone action, first, by determining which cells are to manufacture which hormones. and second, by determining which hormones, and what quantities of them, are to be admitted into every cell through the plasma membrane. Genes regulate vitamin action by controlling the manufacture of these substances within cells, and again by regulating surface absorption in cells which do not synthesize vitamins on their own. Control of surface absorption also accounts for gene control over the inorganic constituents of cells.

Fourth, by governing synthesis in general and production of new genes in particular, genes direct growth, development, and the reproduction of cells. By being exchanged among cells and pooled within cells, as we shall see, genes become the basis of sex. By duplicating and being transmitted to offspring cells, genes become the basis of heredity. Moreover, through one final property, genes become the key to evolution.

This final property is mutability, the capacity to mutate. Genetic nucleoproteins are among the most stable of all organic compounds. Indeed, unless an information carrier were relatively stable, it would cease to be useful as a repository of important information. In addition to this inherent chemical stability, genes are protected also by the nucleus, as noted. Another safeguard against loss or alteration of genetic messages is redundancy: genetic information is stored in more than one place. Each cell of most organisms ordinarily contains two complete sets of genes, one set having been inherited originally from the mother of an organism, the other from the father. Hence the even number of chromosomes in most species. Moreover, each cell type is usually represented by many like cells; thus even

if some cells die, the genes of the remaining cells still possess the specific information characteristic of that cell type.

Yet despite inherent stability, protected existence, and redundancy, structural change is bound to occur. For genes are no more exempt from the modifying impact of the environment than any other component of the earth. A variety of physical and chemical agents may affect and alter gene structure, and therefore gene specificity. Such new specificities will themselves be stable and will be passed on into all subsequent gene duplicates. Protein synthesis will be affected accordingly, and as a result, cell traits will become changed. *Mutations* of this sort are the basis of evolution, as we shall see.

In summary, therefore, we find that genes serve in just one primary role: they allow their specificities to be copied. Three indirect secondary roles emerge from this: genes control protein specificities; genes control the specificities of new genes; and to the extent that gene stability is imperfect, genes may change their specificities. Through these three secondary activities, genes indirectly govern tertiary functions which encompass every aspect of living. For by controlling all metabolism and all selfperpetuation, genes govern cell structure, cell function, and cell development. And by controlling cells, genes govern the life of all organisms, hence the survival of the whole living world. Genes started life, genes still continue it, and by their failure or absence, genes ultimately end it (Fig. 16.7).

Directed by genes and carrying out genetic commands, other agents in cells play important subordinate roles in steady-state maintenance. *Vitamins* and *hormones* are two of these, and we now proceed to a brief examination of their functions.

VITAMINS AND HORMONES

Whenever a component of a protoplasmic control system becomes abnormally overactive or underactive, *unsteady* state, or disease, is likely to follow. Inasmuch as abnormal functions often give clues to

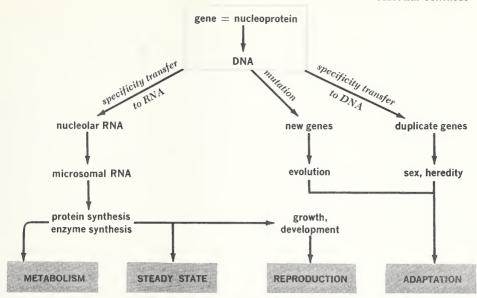


FIG. 16.7. Overall summary of the pattern of gene action. Through their primary action of transferring their specificities, genes control cellular metabolism and all phases of cellular self-perpetuation.

normal functions, diseases are sometimes produced deliberately, by experimental means, in attempts to study the normal roles of particular control components.

The functioning of cellular controllers has been investigated extensively by this means. For example, the action of given genes has been analyzed by the production of genetic deficiencies in cells, that is, experimental alteration, or complete removal, of chromosome sections in which the genes under study are located. Similarly, enzyme functions have been elucidated by use of enzyme inhibitors. Or again, by withholding inorganic substances from a cell, nutritional deficiencies may be produced which may reveal the normal roles of the deficient agents.

Above all, the experimental production of deficiencies, and also of excesses, has provided the bulk of our knowledge about vitamins and hormones.

Vitamins

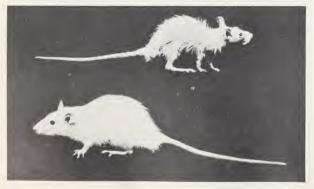
Most cell types synthesize at least some vitamins. Plant cells produce all they require, but animal cells generally do not manufacture enough, or not all necessary kinds. Insects, for example, may synthesize all except the B vitamins. A few rodents, apes, and man cannot manufacture their own vitamir C, but other animals can (hence tigers and lions, for example, may omit orange juice from their diet).

These differences between various animal species, and between animals as a whole and plants, are probably a result of mutation and evolution. Originally, all organisms undoubtedly were able to produce all vitamins on their own. If a random mutation subsequently prevented an autotroph from synthesizing one or more of the vitamins, that

organism could not have survived since, by definition, the autotroph could not obtain the missing nutrients in any other way. But a similarly affected heterotroph still could obtain prefabricated vitamins from other organisms. That mutations may indeed destroy vitamin-synthesizing capacity can be demonstrated experimentally.

More than 30 compounds are known to possess the properties of vitamins; that is, they are required in very small amounts, and their prolonged absence produces deficiency diseases and impairment of metabolic processes in cells. As noted above, the normal roles of vitamins have become known largely through study of vitamin deficiencies. In such studies, careful distinction is made between the clinical and the biological effects of deficiency. For example, it has been known for some time that thiamine deficiency in man may lead to beriberi. This is a clinical result; beriberi is a disease characterized grossly by nervous and muscular paralysis. The implication might be that thiamine normally plays a special controlling role in nerve and muscle

FIG. 16.8. Some effects of riboflavin deficiency. Top: riboflavin-deficient rat. Pronounced loss of hair, sickly appearance. Weight 63 g. Bottom: same rat as above, 6 weeks later, after riboflavin-rich diet. Recovery complete. Weight 169 g. Note that this only illustrates the clinical effect of the vitamin. Experiments of this sort do not reveal the biological effect, i.e., in this case, the hydrogen-transferring role of riboflavin (flavoprotein) in respiration. (Bureau of Human Nutrition and Home Economics.)



cells only. Actually, however, thiamine, and indeed *all* vitamins, are probably required in *all* cells, plant or animal. In the case of thiamine, we already know that this vitamin is essential in the conversion of pyruvic to acetic acid in *all* cells (Chap. 13). It happens that the gross effects of a deficiency may show first, or most pronouncedly, in a particular group of cells, nerves and muscles, for example. But such clinical results are merely the visible secondary consequences of deeper effects of deficiency, influencing all cells universally. It is these which are of basic biological significance. Clearly, clinical results are the beginning, not the end, of vitamin studies (Fig. 16.8).

When first investigated, vitamins were given letter designations in alphabetical order. Later, virtually every vitamin so labeled was found to consist not of one but of several, often related substances. Letters with subscripts then came into use. Today, the tendency is to refer to a new vitamin by its chemical name only. Many vitamins therefore do not have a letter designation, and some have both letter and chemical labels.

Vitamins as a whole may be classified as <u>fatsoluble</u> or <u>water-soluble</u>. The former group includes vitamins A, D, E, and K, the latter, vitamins B and C. In animals, all fat-soluble vitamins require bile for proper absorption from the gut, and whenever fat digestion is impaired, or when fats are rigidly excluded from the diet, vitamin deficiency develops easily. Water-soluble vitamins frequently pass into cooking water and into the water surrounding canned food; hence such juices should not be thrown away.

The names, food sources, and cell functions of the most important vitamins, and the clinical effects of deficiency, are listed in Table 8. To a variable extent among animals, adequate supply of vitamins depends directly on adequate nutrition. In all animals and all plants, the supply of hormones, on the other hand, hinges primarily on internal secretion.

Plant hormones

The best-known plant hormones are called auxins. They are secreted by shoot meristem tissue, and

TABLE 8. The principal vitamins and their functions

Name		Source		Chief functions	Effects of deficiency
Vitamin A		Leaves, yellow foods, carotene, liver		Chemistry of vision; mem- brane integrity	Night blindness; infectious diseases; bone, nerve ab- normalities
Thiamine (B ₁) Riboflavin (B ₂) Nicotinic acid Pantothenic acid Folic acid Vitamin B ₁₂ Biotin Choline Pyridoxine (B ₆)		Grain products, yeast, beans, nuts, liver, eggs, meat	}	Pyruvic acid \rightarrow acetic acid Aerobic H transfer DPN precursor Acetic acid metabolism Nucleic acid metabolism CO_2 metabolism Fat, protein metabolism	Beriberi Hair loss; growth failure Pellagra Anemia; growth failure; hemorrhages; bone disorders; nerve, skin disorders; infectious diseases
Vitamin C		Citrus fruits, tomatoes		Amino acid combustion; synthesis of cell "cement"	Scurvy
Vitamin D		Liver, fish oils		Ca and P regulation	Rickets
Vitamin E Vitamin K	}	Most foods	}	Aerobic H transfer	Sterility; eye abnormalities; nerve, muscle disorders Failure of blood clotting

their central function appears to be the regulation of water metabolism in plant cells. When auxin is present in a plant cell, that cell takes up increased amounts of water and, in parallel with this, the cell enlarges. This basic growth effect has important consequences, for it leads to varied plant behavior in response to different environmental stimuli.

Such behavior responses are thought to be a result of (1) the destruction of auxin by light and (2) the ready diffusibility of the hormone from cell to cell. Suppose that an upright shoot is illuminated only on the left side and is kept in comparative darkness on the right. Much of the hormone secreted on the left side of the shoot tip is destroyed before long by light. But on the right side, the auxin persists. Hence shoot-tip cells on the left do not grow so much as those on the right. The tip consequently bends over to the left. In other words, the plant acts as if it were "aware" of the position of the light and grows toward it (Fig. 16.9).

A plant in an open field is illuminated more or less equally from all sides. Some auxin is therefore destroyed on all sides, and the shoot grows straight up. But it does not grow as much as if it were kept in darkness. Let an onion or a potato sprout in a dark cellar and another one on a window sill; observe the size difference of the sprouts after a few days. Of course, in the prolonged absence of light, growth cannot continue indefinitely. A dark-grown plant will die after stores of food reserves are exhausted. Under normal field conditions, plant growth is a compromise between stimulation by light, via photosynthesis, and inhibition by light, via auxin destruction.

Other control functions of auxin do not always involve growth. But like growth control, all such other functions probably trace to regulation of water metabolism also. Here may be mentioned the prevention of premature shedding of leaves and the dropping of fruits; the initiation of fruit develop-



FIG. 16.9. This plant was illuminated only from the top left. Note the bending of the stem in the direction of the light source. (Courtesy of W. G. Smith, Jr., and Boyce Thompson Institute for Plant Research.)

ment by auxins released from pollen; and the control of fruit ripening. Although the mechanisms of control in most of these instances are still relatively obscure, the very fact of auxin involvement has been turned to important horticultural advantage. For auxin can be extracted and can be applied to economically significant plants in the form of sprays or salves. Moreover, some 30 other substances have been found which do not occur naturally in plants but which are auxinlike in their effects. Such artificial hormones may be applied to plants instead of auxin.

For example, by judicious use of hormone sprays, the rate of fruit ripening and the time of fruit drop can be adjusted to some extent. Thus, if a fruit-bearing branch is moderately constricted at its base, auxin diffusion out of the branch is partially prevented. The accumulating hormone, and probably also the accumulating sugars, may produce larger fruits. Auxins are also used as weed killers. Certain hormone concentrations are only mildly stimulative

or are indifferent to lawn grass, but are overstimulative to many weeds. Sprayed weeds then metabolize so intensely that they almost literally burn themselves out and die.

Animal hormones

In animals, as in plants, a hormone is a substance secreted by a cell, carried in the body fluids, and used by another cell. Among animals, hormone-secreting cells are usually located within distinct, specialized endocrine glands. Actually, only two animal groups are known to possess such glands, the *insects* and the *vertebrates*.

The hormones of insects and vertebrates vary greatly in chemical composition. Some are proteins,

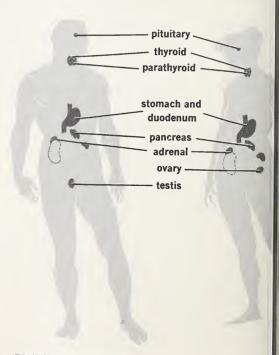


FIG. 16.10. The endocrine system.

some are amino acids, some are sterols, some are other simple or complex kinds of compounds. A few can be synthesized in the laboratory, a few have a known chemical structure, and the remainder are known only through their clinical effects. Such effects become evident through hormone deficiency (e.g., undersecretion, excision of the secreting cells) or through hormone excess (e.g., oversecretion, injection of hormone).

Like the auxins of plants, insect hormones are essentially growth promoters. They initiate and control the development of larvae, the transformation of larvae into pupae, and the final transformation of either larvae or pupae into adults. Beyond these very basic developmental functions, little is known about the cellular, metabolic roles of the hormones. In vertebrates, on the other hand, the cellular functions of hormones may be circumscribed rather well, although the precise reactions in which hormones play parts cannot yet be pinpointed as well as for many vitamins. For example, there is no doubt that the thyroid hormone promotes respiration, but what specific reaction or reactions are affected are still obscure.

Just as all cells probably require all vitamins, so also all mammalian cells probably require all hormones. The term "sex hormone," for example, is somewhat misleading. True, sex hormones are manufactured in sex organs and contribute to their proper function. As we now know, however, these hormones also contribute to the functioning of practically every other organ in the body. It happens that the effect of deficiency or excess of a given hormone may show first, or most obviously, in a particular group of cells. We may infer from this that in these cells the hormone probably regulates a specialized function. We may, for convenience, name the hormone according to this function, but we cannot conclude this role to be its only one, or even its most fundamental one.

Apart from their other controlling function in cells, many vertebrate hormones have an additional special function: they control the manufacture and



FIG. 16.11. Longitudinal section through a human pituitary gland. The right side of the photo points in the direction of the face; the left side, in the direction of the back of the head. Note the anterior lobe in the right part of the gland and the intermediate and posterior lobes in the left part. The anterior lobe secretes hormones such as TTH (see also Table 9). The posterior lobe continues dorsally as a stalk which joins the whole gland to the brain. (Courtesy of Dr. B. J. Serber, College of Medicine, New York University.)

secretion of one another. Thus many endocrine glands cannot secrete their hormones unless they are simulated to do so by other hormones, from other endocrine glands. The entire endocrine organ system (Fig. 16.10) in effect functions like a board of directors in which the members hold one another in close mutual check. The output of each gland is controlled, wholly or partially, by the output of one or more other glands. And as a result, the overall output by all glands is carefully balanced. This is essential, for whereas one hormone may accelerate a given cellular process, another hormone may inhibit the same process. Hence, unless the

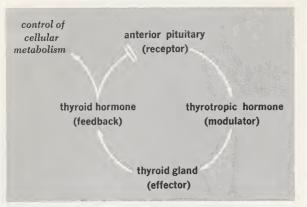


FIG. 16.12. The action of certain pituitary hormones and their feedback control. Pituitary-thyroid interaction is shown as an example. Pointed arrows symbolize stimulation, and the arrow tipped with a transverse double bar symbolizes inhibition. Through this control cycle, the output of thyrotropic hormone is automatically self-adjusting.

amounts of hormones are continuously readjusted relative to one another and relative to the requirements of the moment, flexible control over cellular processes would not be possible.

This "checking" action of one endocrine gland by another is illustrated well in the case of the pituitary and thyroid glands. The pituitary (Fig. 16.11) secretes a hormone known as the thyrotropic hormone, TTH for short. The only known function of this hormone is to stimulate the thyroid gland. Without TTH, the thyroid is inactive; with TTH, the thyroid is stimulated to secrete its own hormone, called thyroxin (or simply "thyroid hormone"). We already know that thyroxin controls the rate of respiration. But thyroxin also has one other function: it acts on the pituitary and inhibits it. Therefore, when thyroxin reaches the pituitary, the output of TTH by that gland will be reduced or even stopped. And since TTH is required for thyroid secretion, reduced TTH output by the pituitary will also reduce the thyroxin output. But less thyroxin will mean that it will inhibit the pituitary less, which in turn means that the pituitary can again produce more TTH. The net effect of these successive stimulations and inhibitions is that the hormone output of both pituitary and thyroid is controlled and actually is kept relatively constant. Indeed, the two glands and their two hormones form an automatic, self-adjusting control system with built-in feedback. Through such control, the thyroid, for example, can secrete neither too little nor too much of its hormone (Fig. 16.12).

We may note here that the pituitary gland also interacts in similar manner with the cortisone-producing adrenal gland (specifically, the adrenal cortex) and with the sex-hormone-producing ovaries and testes. We shall have occasion to discuss these sex-hormone effects in Chap. 21.

The names, glandular sources, and the main functions of the chief hormones, as well as their clinical effects in deficiency or excess, are listed in Table 9.

This completes our discussion of controlling agents operating primarily within cells. The next chapter will deal with agents exercising control among cells, i.e., with tissue- and organ-level controllers.

REVIEW QUESTIONS

- 1. In what different ways may one define "gene"? Why does a single definition not suffice? Where in a cell are genes found? Be specific. Where in a cell do (a) DNA and (b) RNA occur?
 - 2. Review the kinds of chemical components present

in nucleoproteins, and specify the particular kinds present in genetic nucleoproteins. How do DNA and RNA differ chemically? Describe the Watson-Crick model of gene structure. What probably accounts for the specificities of different DNA's?

Effects of deficiency

TABLE 9. The principal endocrines and their hormones

Gland	Hormones	Chief functions	or excess
Pituitary, anterior lobe	Thyrotropic Gonadotropic ACTH Lactogenic Growth	Stimulates thyroid Stimulates gonads Stimulates adrenal cortex Stimulates milk secretion Promotes cell metabolism	Dwarfism; gigantism; acromegaly
Pituitary, mid-lobe	Intermedin	Controls adjustable skin-pig- ment cells (e.g., frogs)	
Pituitary, posterior	At least five distinct fractions	Controls water metabolism, blood pressure, kidney func- tion, smooth muscle action	Excessive water excretion
Thyroid	Thyroxin	Stimulates respiration; inhibits thyrotropic secretion	Goiter, cretinism; myxedema
Parathyroid	Parathormone	Controls Ca metabolism	Nerve, muscle abnormali- ties; bone thickening or weakening
Adrenal cortex	Cortisone, other sterol hormones	Controls metabolism of water, salts, carbohydrates, fats, proteins; inhibits ACTH secretion; duplicates sex- hormone functions	Addison's disease
Adrenal medulla	Adrenalin	Alarm reaction, e.g., raises blood pressure, heart rate	Inability to cope with stress
Pancreas	Insulin	$Glucose \rightarrow glycogen$	Diabetes
Testis	Testosterone, other androgens	Promote cell respiration, blood circulation; maintain primary and secondary sex	Atrophy of reproductive system; loss of secondary sex characteristics
Ovary	Estradiol, other estro- gens	characteristics, sex urge; in- hibit gonadotropic secre- tions	

302

- 3. What appears to be the fundamental function of genes? In what sense may gene function be considered to be passive?
- 4. What two kinds of specificity transfers do genes participate in, and when do these transfers occur? What is the template hypothesis, and what is it designed to explain? Review in detail the possible mechanism of specificity transfer from DNA to DNA, based on the Watson-Crick model.
- 5. Review the pattern of processes by which genes control (a) cellular metabolism, (b) other cellular controllers, including other genes, and (c) all aspects of self-perpetuation. How is the stability of genes safeguarded? What is the importance of gene stability? What is the effect of alterations in gene structure?
- 6. What is a vitamin? Review the function of three vitamins. Distinguish between clinical and biological effects of vitamin or hormone deficiencies. Different animals must be supplied with different vitamins. Why? How did these differences probably arise?
- 7. Describe the role of auxins in plant growth and growth behavior. How do shoots grow toward light regardless of their original orientation? In what processes other than growth do auxins play a role?
- 8. What is a hormone? How do given endocrine glands control the activity of other endocrine glands? Show how the activity of the adrenal cortex is regulated by the pituitary, and vice versa.

SUGGESTED COLLATERAL READINGS

- Biale, J. B.: The Ripening of Fruit, Sci. American, vol. 190, 1954.
- Constantinides, P. C., and N. Carey: The Alarm Reaction, Sci. American, vol. 180, 1949.
- Crick, F. H. C.: The Structure of the Hereditary Material, Sci. American, vol. 191, 1954.
- Funkenstern, D. H.: The Physiology of Fear and Anger, Sci. American, vol. 192, 1955.
- Gamow, G.: Information Transfer in the Living Cell, Sci. American, vol. 193, 1955.
- Greulach, V. A.: Plant Movements, Sci. American, vol. 192, 1955.
- Horowitz, N. H.: The Gene, Sci. American, vol. 195, 1956.
- Ingram, V. M.: How Do Genes Act? Sci. American, vol. 198, 1958.

- Jacobs, W. P.: What Makes Leaves Fall, Sci. American, vol. 193, 1955.
- Levine, R., and M. S. Goldstein: The Action of Insulin, Sci. American, vol. 198, 1958.
- Li, C. H.: The Pituitary, Sci. American, vol. 183, 1950.
- Mirsky, A. E.: The Chemistry of Heredity, Sci. American, vol. 188, 1953.
- Nayler, A. W.: The Control of Flowering, Sci. American, vol. 186, 1952.
- Salisbury, F. B.: Plant Growth Substances, Sci. American, vol. 196, 1957.
- Schocken, V.: Plant Hormones, Sci. American, vol. 180, 1949.
- Taylor, J. H.: The Duplication of Chromosomes, Sci. American, vol. 198, 1958.
- Zuckerman, S.: Hormones, Sci. American, vol. 196, 1957.

CHAPTER 17

The body fluids

Cells are in steady state relative to their immediate environments. In a multicellular organism, these environments are other cells, which are components of tissues, organs, and organ systems. It follows that each organ system contributes to the steady state of every other system and, in turn, is maintained in steady state by every other system. For example, the steady-state function of the digestive system is to provide an adequate supply of nutrients for all other systems. But the digestive system is itself kept in steady state by the nervous system, the circulatory system, and by every other system as well. No one system can therefore

be said to be "more important" than any other, for each fulfills a necessary role.

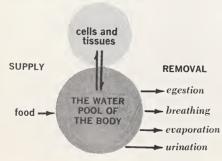
Four systems in particular exercise their controlling functions more widely throughout the body than any others, and they are therefore required most critically and directly in steady-state maintenance. These four are the *breathing*, the *circulatory*, the *excretory*, and the *nervous* systems. Other systems may suspend operations temporarily, and the organism may yet survive: muscles may become paralyzed, food may be unavailable, reproduction may cease, skin may be burned, bones may be broken; these and similar conditions may well be extremely damaging, but they need not be lethal. By contrast, stop breathing, stop the heart, stop kidney function, stop brain function—any one alone will bring death almost immediately. This indicates clearly that these four systems exercise controls without which the organism cannot do even briefly. Their constant operation is vitally necessary if immediate and irreversible unsteady state is to be avoided.

The function of breathing has already been discussed in Chap. 12, and the operations of the nervous system will be discussed in the following chapter. Here we deal with the circulatory and the excretory systems. Both control the attributes of the body fluids, i.e., blood and lymph, which permeate the entire body and determine the immediate environment of every cell. The circulatory system carries the body fluids and governs their physical character—pressure, distribution, rate of flow. The excretory system governs the chemical character of the fluids—which materials are and which are not to be retained in them.

BLOOD AND LYMPH

The expression that a certain personality trait "is in one's blood"; phrases like "hot blood," "bad blood," "blue blood"; and race doctrines based on

FIG. 17.1. The water balance of the body. Under normal conditions, supply and removal are adjusted for maintenance of a constant water content within the body.



alleged blood differences; all trace back to primitive notions of ancient and medieval philosophers. They believed that blood, together with "phlegm," "yellow bile," and "black bile," constituted four "humors" which, mixed in various proportions, determined the nature of man. We know today that the gall bladder and its bile can be removed surgically, that blood can be drained off and replaced by blood from another person, yet the nature of man changes not one whit. Moreover, in the healthy person, blood is neither hot nor cold, but is always maintained at a constant temperature of 37°C. Blood is not blue but red; and from one race to another, blood chemistry differs no more than between extremes within a given race. The nature of man, and of animals generally, is determined in part by genes and in part by environment, never by blood.

Blood is a *tissue*. It is composed of loose cells and of plasma, a fluid in which the cells are suspended. Approximately half of the blood of a mammal is cellular, the other half plasma.

Blood plasma

The main constituent of plasma is water. Its source is food and metabolic water excreted by cells into the body fluids. The supply of water is carefully counterbalanced by excretion, through lungs, sweat glands, and kidneys. The total water content of the body, hence blood volume, is thereby maintained constant (Fig. 17.1).

Blood water has many functions. From this store, cells draw their own protoplasmic water. Oozing out from capillaries as the main constituents of lymph, blood water envelops all tissues of most animals, in the same way that ocean water enveloped the cells of their primitive ancestors. By its very presence in a certain quantity within a closed channel system, blood water contributes importantly to blood pressure. After extensive blood loss through wounds, one of the foremost requirements is restoration of blood volume, that is, restoration of water.

Blood water is the transport vehicle for all other

plasma components and for blood cells. Dissolved or suspended in blood water, apart from cells, are two groups of substances. One consists of materials normally maintained at *constant* concentrations. This group includes inorganic ions, plasma proteins, and other organic materials which might be nutritional raw materials in transit to cells, such as glucose or waste products in transit to the kidneys.

Constancy of such components is achieved by balancing supply against removal. Supply may take the form of absorption from the gut, or release by tissue cells, or manufacture and release by the liver. Removal may involve liver storage, excretion from kidneys and a variety of other organs, or absorption by tissue cells. In each case, too high or too low a concentration of a given substance in the blood is the critical stimulus for its own removal or replenishment. As we have seen, for example, a high blood-glucose level stimulates liver cells to lower it, by storing the excess as glycogen. Activities of this sort, performed by various organs, bring about a steady state in blood.

The second group of plasma constituents consists of substances which fluctuate more or less widely in concentration, depending on body activity. In this category are a number of foods in transit, urea and other waste products in transit, hormones in transit, and many other substances.

Each of the plasma substances serves one or more functions. For example, inorganic ions and blood proteins of all kinds aid in maintaining a constant blood pH (normally 7.3) and a constant osmotic pressure. Some of the blood proteins also function in blood clotting (see below), and others serve as defensive antibodies, which destroy infecting bacteria or render them harmless (Fig. 17.2). Certain of the blood proteins are the basis of differences in blood type. Table 10 lists the main components and functions of blood plasma.

Clearly, this fluid plays many roles in body-wide steady-state maintenance. It serves as a sensory and motor path interconnecting all cells. It is a modulator contributing to the physical and chemical constancy of all tissues. And it is a receptor of infectious stimuli and a defensive effector against them. All this is in addition to the purely transportive functions of plasma, namely, delivering nutrients and collecting wastes, and in addition also to the function of plasma as lymph, through which it provides a proper operating environment for all cells.

Blood cells

Three kinds of cellular components are found in blood: red corpuscles, white blood cells, and blood platelets (Fig. 17.3).

The major function of the *red corpuscles* is their transporting of oxygen (Chap. 12). In the adult

TABLE 10. The principal constituents and functions of blood plasma*

Components	Functions		
1. Water	Maintains blood vol- ume, pressure; forms lymph; water supply of cells; vehicle for other constituents		
2. Inorganic ions	Maintain osmotic bal- ance, pH balance; CO ₂ transport to lungs; varied effects on tissue cells		
3. Plasma proteins	All aid in osmotic and pH balance		
Fibrinogen	Participates in blood clotting		
Prothrombin	Participates in blood clotting		
Albumins, enzymes Globulins	Functions obscure Basis of blood types; act as antibodies		
4. Glucose, other organic materials	In transit to and from cells		
5. Urea, CO ₂ , O ₂ , foods, hormones, vitamins, and others	In transit to and from cells		

[•] Categories 1 to 4 are maintained at constant concentrations; materials in category 5 occur in variable concentrations.

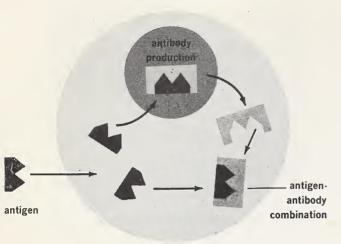


FIG. 17.2. The action of specific antibodies. A foreign protein introduced into an organism is an antigen. It elicits the formation of antibodies, i. e., special proteins in blood plasma, which "fit" precisely the surface configuration of the antigen. These specific antibodies may then combine with the antigens, making the latter harmless.

vertebrate, red corpuscles are manufactured in the red marrow at the ends of long bones (e.g., ribs, arms, legs). Liver and spleen are the production sites in the embryo, before bones mature. After the skeleton is fully formed and blood-cell production is initiated in it, the spleen becomes principally a blood-storing organ. It may contract and like a sponge squeeze reserve blood into the circulation. The liver becomes the organ where red corpuscles are destroyed.

Production in bone marrow is so geared to destruction in the liver that the number of red corpuscles is kept fairly constant. The controlling signal is the amount of oxygen carried by blood (Fig. 17.4). Low oxygen content stimulates bone marrow to produce red corpuscles at a faster rate. At the same time, the liver is inhibited from destroying corpuscles at too fast a rate. Hence when inhaled air contains too little oxygen for extended periods, as at high altitudes, then more corpuscles

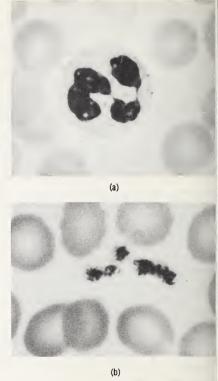


FIG. 17.3. Human red blood corpuscles are shown in both photos. Note absence of nuclei. A white blood cell (nucleated) is shown in center of (a) and a few blood platelets in center of (b). (General Biological Supply House, Inc.)

are manufactured. An adequate quantity of gas thus may still be delivered to the tissues by this greater number of corpuscles. A persistently high oxygen concentration in blood has the opposite effect on liver and bone marrow.

In man, each cubic millimeter of blood, roughly the volume of a pinhead, contains over 5 million red corpuscles. It has been estimated that every second some 10,000 corpuscles are manufactured and an equal number are destroyed. In mammals, but not in other vertebrates, maturation of a red corpuscle in bone marrow involves the disintegra-

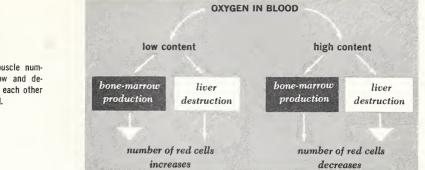


FIG. 17.4. Control of red corpuscle number. Production in bone marrow and destruction in liver are geared to each other by the oxygen content of blood.

tion of the cell nucleus. Thus mature corpuscles in the mammalian blood stream are without nuclei (hence the designation "corpuscles" rather than "cells").

White cells (Fig. 17.3) are transparent and colorless. Two groups may be distinguished, leucocytes and lymphocytes, each consisting of a number of subgroups. These various types are distinguished on the basis of cell structure, size, origin, and function. All white cells possess nuclei, but they normally do not divide.

Leucocytes are manufactured in red bone marrow, probably by the same generating tissue which also gives rise to red corpuscles. Lymphocytes are formed in lymphatic tissue, principally the lymph nodes found along the path of lymph vessels. Lymphocytes reach the blood stream via the lymph channels. Altogether, white blood cells are much less abundant than red corpuscles. A cubic millimeter of human blood contains about 8,000 white cells.

To greater or lesser degree, all white cells, but leucocytes particularly, are capable of ameboid locomotion. Like amebae, they extend pseudopods into which the rest of the cell flows. By this means, they are able to squeeze through blood capillary walls, passing in between neighboring cells in the walls (Fig. 17.5). Once out in the tissues, they migrate toward sites of infection, and there they engulf and

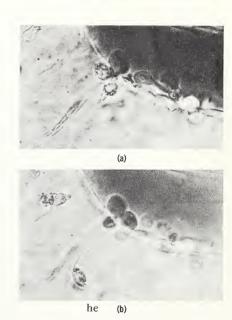


FIG. 17.5. The migration of blood cells through capillary walls. In each photo, a blood-filled capillary is in upper right portion. (a) Two white blood cells have just penetrated through the capillary wall into surrounding tissues, and a red corpuscle is halfway through the capillary wall. (Courtesy white cells have migrated farther into the tissue, and the red corpuscle is halfway through the capillary wall. (Courtesy of Dr. R. Brenner, Brown University.)

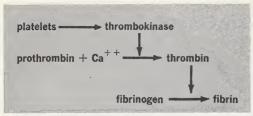


FIG. 17.6. The main features of the clotting reaction.

digest bacteria, in the same way that an ameba engulfs and digests food. Accumulations of white cells, bacteria, and the debris from infected tissue constitute pus. We note that the principal function of white cells is internal body defense.

Platelets (Fig. 17.3) are not cells in the usual



FIG. 17.7. The human heart. The large blood-vessel stump is the aorta. The auricles are partly hidden by the aorta. The size of your fist is very nearly the actual size of your heart. (Photographic Department, Rhode Island Hospital.)

sense, but are probably cell *fragments*. They are tiny bits of protoplasm surrounded by a membrane, and nuclei are often absent. About one-quarter million of these bodies are found in each cubic millimeter of human blood. Platelets are manufactured predominantly in red bone marrow and to some extent also in the connective tissue of the lungs.

Platelets are essential in blood clotting. This self-sealing mechanism of the circulatory system is brought into action whenever platelets encounter obstructions which rupture them. In most cases, such obstructions are the rough edges of torn blood vessels. External clotting then occurs. But roughness of the inner surfaces of blood vessels, produced, for example, by solid deposits, as in hardened arteries, may suffice for the rupturing of platelets too. An internal blood clot may then form.

The clotting process is exceedingly complex, and the complete sequence of events is not yet established. However, an abbreviated, simplified account may be given to indicate what takes place (Fig. 17.6). Among the materials oozing out from ruptured platelets is an enzymatically active substance, thrombokinase, also called thromboplastin. This substance interacts with two components of blood plasma: calcium ions and prothrombin, which is one of the plasma proteins. Prothrombin is an inactive precursor of the catalyst thrombin. Thrombokinase, in the presence of calcium ions, converts prothrombin to thrombin. Thrombin subsequently reacts with fibrinogen, another of the plasma proteins. As a result of the reaction, fibrinogen becomes fibrin, an insoluble protein. Fibrin constitutes the blood clot. It is a yellowish-white meshwork of coagulated protein, in which blood corpuscles are trapped. Hence the redness of the clot.

Clotting can be prevented when any of the ingredients are missing or are made inoperative. For example, fibrinogen can be withdrawn fairly easily from whole blood or plasma. This procedure is often used in storing blood or plasma for transfusion. Plasma minus fibrinogen is called blood serum.

We note that blood as a whole forms the first line of internal defense. However, this control function of blood, as well as its other functions in transport and tissue maintenance, can be exercised only if blood *circulates*. Consequently, as tissue functions are dependent on blood, so blood functions in turn are dependent on the transport channels.

CIRCULATION

This composite activity is carried out by the heart, the blood vessels, and the lymph vessels. These organs represent more than a pumping station and a system of pipes, for they also regulate the speed and force of motion and the distribution of the moving fluids.

It should be kept clearly in mind that from the standpoint of individual tissue cells, the important parts of the circulatory system are the *capillary vessels*. It is through them, and only through them, that circulating body fluids sustain the life of cells. Vital exchanges of information and of materials between blood and tissue cells occur only in the microscopic capillaries. But to make such exchanges possible, structures like heart and large blood vessels become necessary adjuncts.

The pathway

The heart lies in the mid-plane of the chest, directly underneath the breastbone. But it is tilted somewhat, the lower tip projecting over to the left. This is where the beat of the heart is most readily discernible (Fig. 17.7).

To each of the four chambers of the heart, the right and left auricle and the right and left ventricle, one large blood vessel is connected (Fig. 17.8). The aorta leaves the left ventricle, and its branches supply all parts of the body with arterial (i.e., oxygen-rich) blood. Venous (i.e., oxygen-poor) blood collects from all body regions and returns through the vena cava into the right auricle.

The right auricle connects with the right ventricle through the tricuspid valve, an opening equipped with three flaps which lets blood through from auricle to ventricle but not in the reverse direction. Venous blood collected in the right ventricle.

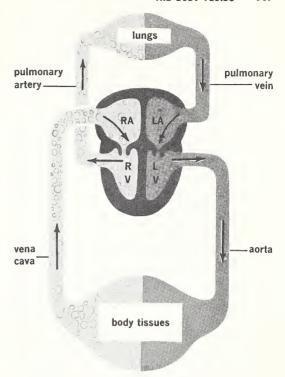


FIG. 17.8. Diagram of the course of blood circulation through the body. Arterial blood is in the left side of the circulatory system (right side of the diagram), venous blood in the right side (left side of the diagram).

tricle leaves this chamber via the pulmonary artery, a vessel leading to the lungs. Here blood is oxygenated, and arterial blood returns through the pulmonary vein into the left auricle.

A bicuspid, or mitral, valve, equipped with two flaps, separates the left auricle from the left ventricle. Like the tricuspid on the right, the mitral valve also opens into the ventricle only. The valve flaps are prevented from letting blood pass in the wrong direction by strands of tissue resembling parachute strings, which attach to the free edges of

the valve flaps on one end and to the ventricle walls on the other (Fig. 17.9). The tricuspid and mitral valves together may be referred to as the auriculoventricular valves, or **A-V valves**.

Smaller valves are situated where the aorta and the pulmonary artery leave the left and right ventricle, respectively. These valves *open away* from the heart and close toward it.

Note that the left chambers of the heart are not connected directly with the right chambers. The left handle arterial blood only; the right, venous blood only. Inasmuch as the auricles pump blood only as far as the ventricles, relatively thin muscular walls suffice. But the ventricles, the left one in particular, pump blood into the farthest parts of the body.



FIG. 17.9. The heart cut open to show the interior of the left ventricle. Note the strands of tissue attached to the two flaps of the bicuspid valve. These strands prevent the valve from opening into the auricle (white area above the ventricle). (Photographic Department, Rhode Island Hospital.)

These chambers possess proportionately thick walls. How does the heart work?

The process

The heart is a pressure pump. It generates pumping force on contraction, or systole, and it rests during muscular relaxation, here called diastole. A complete heartbeat consists of one systole and one diastole, the whole beat lasting about 0.8 sec in a normal human adult at rest. On an average, therefore, 72 beats take place per minute.

A heartbeat starts with the contraction of the auricles (Fig. 17.10). These chambers gradually fill with blood returning via vena cava and pulmonary vein. When they are full, their muscular walls contract. The ventricles are relaxed at that time. As the auricles contract, blood cannot flow backward because incoming blood presses steadily *into* the auricles. Therefore the only path open to auricular blood is through the A-V valves, which lead into the ventricles. These chambers now fill as the auricles empty. The auricular phase of the heartbeat lasts about 0.1 sec. The auricles then relax for the remaining 0.7 sec of the cycle, slowly refilling during this interval in preparation for the next beat (Fig. 17.11).

As soon as the auricles have relaxed, the ventricles, by this time full with blood, contract in their turn. Their thick walls generate much more pressure than the walls of the auricles. Also, ventricular systole lasts longer, namely, some 0.3 sec. As the contraction peak is reached, blood is forced against all ventricular openings, including the A-V valves. But as blood slaps against the A-V flaps, these snap shut and prevent backflow into the auricles (Fig. 17.10). This impact of blood against the valve flaps produces the first heart sound, which can be felt or heard as "the" heartbeat. When the A-V valves are defective, the flaps may not close tightly, and some blood then does flow back into the auricles. This can be heard with a stethoscope and is described as a "heart murmur." Slight murmurs do not impair the efficiency of the heart significantly.

auricular relaxation

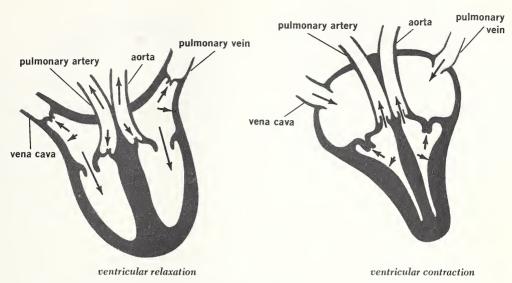


FIG. 17.10. The pumping action of the heart. In the left figure, the auricles are shown contracting, forcing blood into the relaxed ventricles. The A-V valves are open, but the pressure of blood closes all others. In the right figure, the ventricles contract, forcing blood into the pulmonary artery and the aorta. The auricles are relaxed at the same time, filling with blood in preparation for the next beat.

The only way blood can leave the ventricles. normally, is via the aorta on the left and the pulmonary artery on the right. The exit valves into these vessels open as blood presses against them with great force. The sudden quantity of fluid now rushing out dilates portions of the exit arteries adjacent to the heart. But the arterial walls are elastic and snap back into position, thereby adding to the pressure of blood. Most of the blood is thus forced forward, where the open paths lead to the lungs and to all body tissues. But some blood tends to press back into the ventricles. This snaps the exit valves shut, and blood then cannot flow in this direction (Fig. 17.10). The impact of blood in closing the exit valves generates the second heart sound, fainter than the first.

Note that even the ventricles rest more than half the time (Fig. 17.11). Note also that no part of the heart actually is ever empty, but is only more distended or less distended, with blood under greater or lesser pressure. This differential pressure alone determines the position of the heart valves, hence the course in which blood can flow.

Arterial blood "flows" in rhythmic spurts, according to the rhythm of the heart. As each spurt of fluid impinges on the walls of arteries, it gives rise to pulse vibrations. Feel for your neck pulse with the left hand and for your left-wrist pulse with the right hand; notice the time difference between the pulses, as a result of the different distances of neck and wrist from the heart.

With increasing distance from the heart, arterial

spurts become less and less forceful. By the time blood is through capillary vessels and has reached veins, it no longer spurts but flows in a continuous, even stream. The heart here produces very little direct push. Venous blood keeps moving slowly by the push of blood from behind and by contraction of skeletal muscles which squeeze the veins (Fig. 17.12).

The pressure of lymph is even lower than that of blood. Here again, push of lymph from behind and muscular activity provide the major forces which return lymph to the blood circulation (Fig. 17.13).

How is the rhythmic beating of the heart controlled and maintained?

The control

Heart rate. The main nervous regulating center of heart rate is located in the medulla oblongata, a region of the hindbrain which also houses the breathing center. Two pairs of nerves lead from a heart-rate center to the heart (Fig. 17.14). Impulses through one pair accelerate heartbeat; impulses through the other slow it. The accelerator nerves travel through the spinal cord for some distance, emerge in the chest region, and innervate the heart. The inhibitory nerve fibers pass from the heart-rate center into the large vagus nerves. One vagus nerve on each side leaves the hindbrain and runs through

FIG. 17.11. The time relationship between auricular and ventricular beats. Note that the auricles contract and generate pressure when the ventricles are relaxed, and vice versa. Note also that the whole heart is relaxed for half the time of a beat.

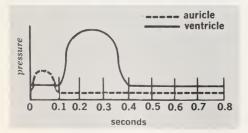




FIG. 17.12. Section through an artery and two veins. Note the thicker wall of the artery and the presence of many elastic fibers (dark wavy lines) in this wall. (Courtesy of Dr. B. J. Serber, College of Medicine, New York University.)

the neck alongside the trachea. Some vagus branches then lead to the heart, others to a variety of organs (e.g., stomach).

Both the accelerator and inhibitor nerves terminate in the wall of the right auricle, at a small patch of specialized tissue called the pacemaker, or sinus node (Fig. 17.14). When the pacemaker is stimulated, a wave of contraction spreads out from it through both auricles. Auricular contraction in turn stimulates a second patch of tissue, the A-V node, situated in the wall which divides the left and right sides of the heart. At the A-V node originates a bundle of modified heart muscle, the bundle of His, specialized for impulse conduction. The strands of this bundle radiate away through the walls of both ventricles. Thus auricular contraction stimulates the A-V node, and impulses transmitted from there through the conductive strands initiate ventricular contraction (Fig. 17.14). The time required for stimulus transmission from

pacemaker to A-V node ensures that the ventricles contract a fraction of a second after the auricles.

The pacemaker is the immediate regulator of heart rate, and the heart-rate center in turn controls the action of the pacemaker. Heart rate, like so many other controlled processes in the body, is a restrained compromise between acceleration and deceleration. Experiments show that decelerating signals via the vagus nerves allow a more flexible adjustment of heart rate than accelerator signals. For example, it can be demonstrated that a speedup of the heart is brought about primarily by a decrease of impulses through the vagus nerves. Thus the heart beats faster mainly because the "brake" has been eased off, not because acceleration has been stepped up. Similarly, a slowing of the heart is mainly a result of increased braking via the vagus nerves.

Blood pressure. If blood pressure becomes too high, thin vessels and the thin-walled auricles of the heart might burst. And if blood pressure becomes too low, blood would not possess sufficient momentum to circulate.

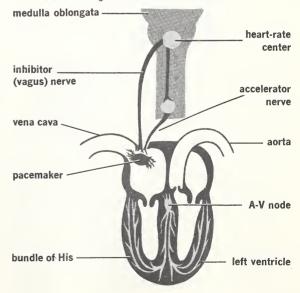
Even in the absence of a pumping mechanism, a quantity of fluid filling a confined space is under a certain pressure. The larger the volume of fluid and the smaller the available space, the greater will be the pressure. Blood pressure therefore depends on three major factors: blood volume, blood vessel space, and, obviously, the force of the heartbeat. A careful distinction should be made between heart *force* and heart *rate*. The heart may beat fast, but feebly; slowly, but forcefully; fast and forcefully; or slowly and feebly.

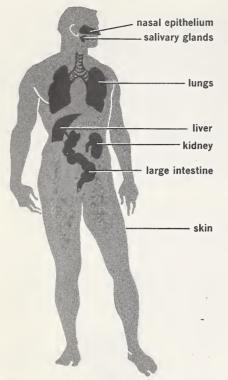
As already noted, blood volume is adjusted through fluid intake and fluid loss. This is a long-range control and, except for contractions of the spleen which put stored blood into circulation, is involved very little in second-to-second regulation of blood pressure. On the other hand, the force of the heart and the space within blood vessels can be varied instantly. These are the significant factors in rapid adjustments of blood pressure.



FIG. 17.13. Longitudinal section through a lymph vessel, showing an internal valve. Such valves prevent backflow. Valves very much like this are present also in the larger veins. (General Biological Supply House, Inc.)

FIG. 17.14. The motor innervation of the heart. Impulses through both inhibitor and accelerator nerves may affect the pacemaker. Impulses from there then stimulate the auricles, as well as the A-V node, which in turn sends signals to the ventricles through the bundle of His.





 ${f FIG.}$ 17.15. Some of the component organs of the excretory system.

In a healthy and properly nourished heart, the force of the beat is determined mainly by the amount of blood received and pumped out in a given span of time. This is a curious but little-understood phenomenon characteristic of all muscle. The greater the work load of a muscle and the more that load stretches it (within limits, to be sure), the stronger is the contraction. Thus when the heart fills slowly and receives only little blood per beat, as under conditions of sleep or complete rest, then its contraction will be relatively weak. But when blood fills the ventricles quickly and to capacity, as during exercise, then the pumping

action will be powerful and blood pressure will increase correspondingly.

The space available within blood vessels is adjusted by contraction and relaxation of the muscles in the vessel walls. *Vasoconstriction* reduces the diameter of blood vessels; *vasodilation* increases it. Vasodilation and vasoconstriction together are referred to as **vasomotion**. These muscular activities are controlled by a **vasomotor center** in the brain, located again in the medulla oblongata, close to the breathing and heart-rate centers. Nerves lead from the vasomotor center to all blood vessels (except the capillaries, which do not possess muscles). Impulses through these nerves to given vasomotor muscles bring about a narrowing or a widening of blood vessels.

Vasoconstriction in all parts of the body simultaneously raises overall blood pressure, and vasodilation lowers it. Vasomotion may also occur in limited regions of the body, leading to a rise or fall of the local blood pressure only. Thus blood pressure can rise in one part of the body and at the same time fall in another part. Through this, also, less blood will flow through one region and more through another. Evidently, vasomotion adjusts not only blood pressure, but also the distribution of blood in the body.

These adjustments are controlled by the vasomotor center, which, like the heart-rate center too, acts in response to various nervous and chemical cues. Nervous cues are exceedingly numerous. Virtually any nervous signal reaching the brain is likely to have an effect on both the heart-rate and the vasomotor centers. For example, pain, emotions, and stresses, all generally tend to affect heart rate, blood pressure, and vasomotion. For example, when an organism sustains a wound, heart rate and overall blood pressure usually rise but the wounded area swells through local vasodilation. The adaptive advantage of this is clear. A rise of heart rate and overall blood pressure produces a state of readiness through faster food flow and oxygen flow to the cells, and this enables the organism to combat stress more effectively. And a local vasodilation in the stressed region itself permits more blood to flow into that region; hence more nutrients and oxygen become available there.

Apart from hormones like adrenalin and other drugs, the chief chemical cue to which the vasomotor system responds is carbon dioxide in blood. If blood reaching the vasomotor center carries a high concentration of CO,, then the center transmits constrictor signals throughout the body. Blood pressure therefore rises. Conversely, low CO2 concentrations bring about a fall of blood pressure. Carbon dioxide also affects the heart-rate center in such a way that high concentrations accelerate heartbeat, low concentrations decelerate it. Moreover, as noted in Chap. 12, high CO2 concentrations also bring about an increased breathing rate. Thus, whenever CO2 needs to be eliminated more rapidly through the lungs, as during strenuous exercise, this waste gas actually controls its own removal: increased breathing and heart rate and blood pressure permit faster collection of CO₂ from the tissues, faster transport, and faster elimination through the lungs.

We note that, through controlled heart rate and blood pressure, the whole circulatory machinery is neatly geared to the varying activities of the body tissues. But control of the physical attributes of the body fluids is only one requirement if these fluids are to service the tissues adequately. A second requirement is control of their chemical attributes, despite changes produced continuously by actively metabolizing tissues. This requirement is met by the excretory system.

EXCRETION

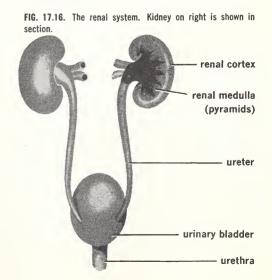
As blood aids in steady-state control of tissues, so the excretory system aids in steady-state control of blood. The excretory system regulates the water content and the blood volume of the body, the pH and the osmotic pressure of blood, and blood chemistry in general. Moreover, through its water-balancing activities, it is also a major regulator of body temperature.

The organs composing the excretory system are shown in Fig. 17.15. We have discussed the excretory action of many of these organs in various earlier contexts. For example, the lungs contribute to elimination of excess water and carbon dioxide. The sweat glands aid in regulating water balance and, to some extent, inorganic ion balance. The large intestine makes a further contribution to ion balance. The liver excretes many diverse materials via bile. And the nasal epithelium, the salivary and the other digestive glands, indeed all the organs with direct access to the exterior of the body, either directly or via the alimentary tract, contribute importantly to excretion.

But the kidneys exercise the major excretory control. When the kidneys are inoperative, all the above organs together are inadequate to prevent death from excretory failure.

Kidney structure

The structure of the mammalian kidney is complex in detail but relatively simple in principle. Each kidney consists of an outer renal cortex and an inner renal medulla (Fig. 17.16). Located partly in



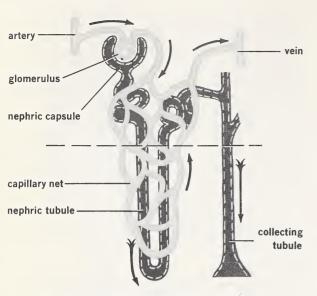


FIG. 17.17. The structure of a nephron and its blood circulation. The portions above the horizontal broken_line form part of the renal cortex (see also Fig. 17.16), and the portions below the line, part of the renal medulla. Flow of urine is indicated by feathered arrows; flow of blood, by plain arrows.

the cortex and partly in the medulla are many thousands of nephrons, the operational units of the kidney (Fig. 17.17).

The most conspicuous component of a nephron is a tube, called the nephric tubule. At one end, this tubule enlarges into a nephric capsule, a structure resembling a hollow ball which has been pushed in on one side until the whole becomes a double-layered cup. At the other end, the nephric tubule leads into a collecting duct, which receives the output of many neighboring nephric tubules. There are many collecting ducts in a kidney. All of them eventually join, forming a wide vessel, the ureter (Fig. 17.16). This channel carries urine into the urinary bladder. A final duct, the urethra, connects the bladder with the outside.

Between the nephric capsule and the entrance into the collecting duct, the nephric tubule is variously coiled and looped. As might be expected, a nephron is in extensive contact with the blood circulation. A large renal artery enters the kidney in the region where the ureter leaves; branches out repeatedly into many smaller arteries; and one of these leads to each nephron (Fig. 17.17). Dipping into the hollow of the nephric capsule, the small artery breaks up into a dense ball of capillaries, called a glomerulus. The capillaries then rejoin into a single vessel, which leaves the capsule and passes into the tubular portion of the nephron. Here this blood vessel branches out once more into a dense capillary net. This net envelops all parts of the nephric tubule. Near the collecting duct, the capillaries lead into a small vein, and many such veins from neighboring nephrons join into larger vessels. All these eventually form a single channel, the renal vein, which leaves the kidney where the renal artery enters.

Kidney function

The standard operating procedure of the kidney might be compared to the work of a pair of hypothetical fish inspectors stationed along the bank of a river. One has a net with which he collects all the fish passing by. The other examines each fish: dead or defective ones he throws away; healthy ones he puts back into the river. Moreover, if there are too many fish altogether, or too many of a particular kind, he may even throw healthy ones away.

In the kidney, the river is the blood stream. The man with the net is the capsule of each nephron. Here blood is filtered through the walls of the glomerular capillaries and the adjacent wall of the capsule (Fig. 17.18).

Filtration requires force. This force is blood pressure. By its agency, every blood component which can go through the glomerular and capsular walls will be pressed into the upper cavity of the nephric tubule. Only two groups of blood constituents normally cannot pass through this filter: blood cells and plasma proteins. All other components do pass

through, without change of concentration. Within the cavity of the nephric capsule will therefore be found blood minus cells and proteins—lymph, or as lymph in this space is commonly called, capsular urine.

Capsular urine passes into the tubular portion of the nephron. The cells composing this tubule represent the second fish inspector of our analogy. These cells share with root-hair cells of plants, mucosa cells of the intestine, and many others the distinction of being more or less a riddle to us. We know in general terms what they do, but not how they do it. Tubule cells are finely selective in their action. On one surface they reabsorb from passing capsular urine a picked group of substances. And on the other surface they secrete these substances back into the blood stream, through the adjacent blood capillary walls (Fig. 17.18). Whatever is not reabsorbed into the blood in this manner constitutes urine, specifically bladder urine, since it is carried through the collecting ducts and the ureters into the bladder.

One of the important substances which the tubule cells reabsorb into the blood is water. In man, all 5 or 6 qt of blood in the body is filtered through the kidneys once every 45 min or so. In a 24-hr period, therefore, the kidneys filter about 150 qt of liquid. Yet in the same period, only about 1½ qt of urine, on an average, is actually excreted by the normal adult. This means that tubule cells reabsorb 99 per cent of the water in capsular urine and leave only 1 per cent as urine.

Another substance always reabsorbed by tubule cells is *glucose*. Capsular urine contains glucose in the same concentration as in blood. But under normal conditions, all the glucose in capsular urine is reabsorbed into the blood and none escapes into bladder urine. Other materials treated similarly include amino acids, fatty acids, glycerin, vitamins, hormones, in short, all the essential nutrients and other usable supplies in transit to cells. These are the "healthy fish" of our analogy.

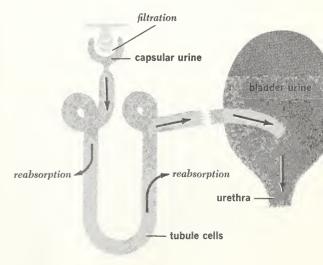
On the other hand, some substances in capsular urine are always left in urine by the tubule cells.

Urea, pigmented blood-breakdown products, and other outright wastes are among these. They become highly concentrated as water is withdrawn from capsular urine. Bladder urine contains some seventy times more urea, for example, than an equal volume of capsular urine.

Note that, as urine becomes more concentrated by withdrawal of water, the osmotic pull of urine becomes greater. But despite this force, which tends to draw water *from* blood into urine, tubule cells nevertheless transport more water from *urine* to blood.

Tubule cells evidently possess exquisite discriminatory powers. They are not only capable of distinguishing one type of molecule from another, but they are also sensitive to concentrations of materials in blood and are able to readjust these concentrations. By now rejecting, now reabsorbing given substances, they are the final arbiters of blood com-

FIG. 17.18. The operation of a nephron. Through filtration of blood, capsular urine is formed, and through reabsorption of various components present in capsular urine, bladder urine is formed.



position.

Thus the kidneys clearly are much more than mere expellers of waste. Indeed, what is or is not "waste" is determined from moment to moment principally by the kidneys. In this, their function of retention is at least as vital as their function of excretion. It may be appreciated why examination of urine will reveal not only how well the kidneys function, but also how well steady state is maintained in the body as a whole.

Urine emerges from the kidneys continuously. The wall of the bladder stretches as urine accumulates in it, and at a certain stage, sensory nerve endings in the wall are stimulated. A reflex initiates contraction of the muscles in the bladder wall, and the organ then empties to the outside.

Excretion, circulation, blood, lymph, and their many controls are means to an end. They enable cells to maintain steady states, and thereby they enable the whole body to maintain steady states. But body fluids are not the only agents exerting control over individual cells; the nervous system is at least as influential. In animals, nerve endings, no less than body fluids, form part of the immediate environment of cells. And cells exchange information and materials with nerve endings just as they do with blood or lymph. Moreover, on the basis of information received and through information sent out, the nervous system harmonizes the various activities of the whole body. We shall discuss these neural operations in the next chapter.

REVIEW QUESTIONS

- 1. Review the composition of blood plasma and the functions of each group of components. What are antibodies? When and where are they produced? How do they act?
- 2. What cellular components occur in blood, and what are the functions of each? By what processes is the number of red corpuscles in the blood maintained relatively constant?
- 3. What are the ingredients required for blood clotting, and through what reactions does clotting take place?
- 4. Name the principal parts of the heart and the principal blood vessels, and review the general course of blood circulation. What structural features distinguish arteries, veins, lymph vessels, and capillaries?
- 5. Review the events during a complete heartbeat, with attention to durations, pressure patterns, valve positions, direction of blood flow, and heart sounds. How is blood moved through veins and lymph vessels?
- 6. Describe the nervous controls of the heart. How are control signals transmitted through the heart itself? Which motor signals accelerate and which decelerate the heart? Through what specific processes is the heart

- speeded up when physical exercise is begun and slowed down during rest or sleep?
- 7. What three major factors control blood pressure, and what governs each of these factors? Describe the action of the vasomotor center. What nervous and chemical agencies affect this center, and how?
- 8. What is the interrelation between vasomotion, heart rate, and breathing rate? Suppose that physical exercise is begun; describe the specific processes leading simultaneously to increased heart rate, increased breathing rate, increased blood pressure, and redistribution of blood within the body.
- 9. What are the overall functions of the excretory system? What organs compose this system, and what is the excretory function of each? Describe the general structure of the kidney and its associated ducts and the specific structure of a nephron.
- 10. Review in detail the process of urine formation. What are the roles of filtration and reabsorption, and where and how does each occur? How does bladder urine differ from capsular urine with respect to the kinds and the concentrations of substances present?

SUGGESTED COLLATERAL READINGS

- Burnet, M.: How Antibodies Are Made, Sci. American, vol. 191, 1954.
- Fox, H. M.: Blood Pigments, Sci. American, vol. 182, 1950.
- McKusick, V. A.: Heart Sounds, Sci. American, vol. 194, 1956.
- Page, I. H.: High Blood Pressure, Sci. American, vol. 179, 1948.
- Ponder, E.: The Red Blood Cell, Sci. American, vol. 196, 1957.
- Smith, H. W.: The Kidney, Sci. American, vol. 190, 1954. Surgenor, D. M.: Blood, Sci. American, vol. 190, 1954.
- Wiener, A. S.: Parentage and Blood Groups, Sci. American, vol. 191, 1954.
- Wood, W. B.: White Blood Cells vs. Bacteria, Sci. American, vol. 184, 1951.

CHAPTER 18

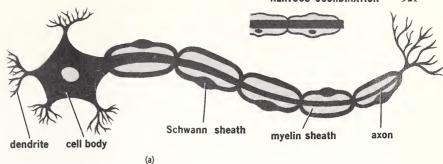
Nervous coordination

Pervous activity is based on *reflexes*. These are the functional units of the nervous system. A reflex is routed through a *reflex arc*, which, like any other control apparatus, consists of five components: receptor, sensory pathway, modulator, motor pathway, and effector.

The neural receptors are specialized cells, which may or may not be housed in elaborate sense organs such as eyes or ears. Receptors translate the energy of incoming stimuli into nerve impulses, and these are transmitted over sensory nerve fibers to the

modulators, namely, brain and spinal cord. Their activity produces new nerve impulses, which travel over motor nerve fibers to the effectors. These are predominantly muscles and glands, and they translate the motor impulses they receive into explicit responses.

Effector functions of muscles and glands have already been discussed in various earlier contexts. In this chapter, therefore, we concentrate primarily on the neural pathways, the neural receptors, and the neural centers.



THE NEURAL PATHWAYS

The mammalian nervous system consists of two subdivisions, the central nervous system (c.n.s.) and the autonomic nervous system (a.n.s.). Brain and spinal cord house the neural centers of both. The c.n.s. largely controls voluntary, conscious activities, and the a.n.s., involuntary, unconscious ones. But the c.n.s. and a.n.s. are highly interdependent and as we shall see, they form a unified, intimately coordinated functional complex.

Regardless of whether reflex activity occurs in the c.n.s. or the a.n.s., the internal working material of the entire nervous system is always the same: nerve cells, which produce and transmit nerve impulses. These properly demand our first attention.

Nerve cells

A nerve cell, or *neuron*, typically consists of a starshaped cell body, containing the nucleus, and of one or more long or short filamentous outgrowths, called nerve fibers, which extend away from the cell body (Fig. 18.1). Nerve impulses normally originate at the terminal of one of the fibers, travel toward the cell body, traverse it, then lead away from the cell body through another of its fibers. Nerve fibers in which impulses travel *toward* the cell body are termed dendrites; those carrying impulses *away* from the cell body, axons. A neuron characteristically possesses only a single axon, but it may have one or several dendrites. By and large, neurons

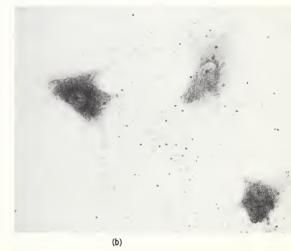


FIG. 18.1. The structure of a neuron. Dendrites may be proportionately longer than shown in the diagram (a). Upper inset: a length of nonmyelinated axon. The photomicrograph (b) shows fixed and stained cell bodies. (Photo, General Biological Supply House, Inc.)

are comparatively huge cells. Dendrites and axons may be as much as a yard or more long, or they may be relatively short.

Long nerve fibers, but not the cell bodies or the shorter fibers, are enveloped by one or by two sheaths. Most of the long fibers of the central nervous system are surrounded directly by a layer of fatty material, the myelin sheath. This sheath in turn is enveloped by what is called the Schwann sheath, which is made up of a single layer of thin flat cells. In most nerve fibers of the autonomic nervous system, only a Schwann sheath surrounds the axon, while myelin sheaths are absent.

Myelin sheaths probably increase the speed of nerve-impulse transmission. It can be shown that myelinated fibers of the c.n.s. may conduct impulses at speeds of about 100 yd per sec, whereas non-myelinated a.n.s. fibers at most conduct at about 25 yd per sec. The suggestion has been made that the accelerating effect of the fatty myelin layer results from an insulating action; a myelin envelope would be to a nerve fiber what a rubber envelope is to an electricity-conducting metal wire.

Individual neurons are placed end to end, forming long neural pathways. The axon fiber of one neuron connects functionally with a dendrite of the next. But there is never a structural connection. Fiber terminals come exceedingly close to one another, yet a microscopic gap, a synapse, still separates them. We shall soon see how nerve impulses are transmitted across such synapses.

Reflex arcs

Pathway patterns. The minimum number of neurons in a reflex arc is two: one sensory neuron, which transmits impulses from a sense organ to

either brain or spinal cord, and one motor neuron, which relays the impulses sent out by brain or spinal cord to an effector organ. Most reflex arcs consist of more than two neurons. One or more additional interneurons may be located within brain or spinal cord, between the end of the sensory and the beginning of the motor neuron. In the entire nervous system, interneurons are actually the most abundant, for they make up the bulk of the brain and the spinal cord (Fig. 18.2).

Sensory neurons leading to, and motor neurons leading from, brain and spinal cord are collected into discrete bundles, which traverse the body like the cables of telephone trunk lines. Such bundles of neuron fibers are nerves. In a so-called mixed nerve, both sensory and motor fibers are present. In certain nerves only sensory fibers are present, and these are called sensory nerves. Analogously, some nerves contain motor fibers only, and they are referred to as motor nerves. Nerves are also classified as cranial or spinal, according to whether they connect with the brain or the spinal cord.

The c.n.s. and the a.n.s. each possess their own set of nerves. Each set connects with distinct c.n.s. or a.n.s. centers in brain and spinal cord, and each of the two subdivisions of the nervous system thus possesses its own reflex pathways.

In the c.n.s., 12 pairs of cranial and 31 pairs of spinal nerves carry information to and from brain and spinal cord. These nerves are named and described in Fig. 18.3. In the c.n.s. nerves, every

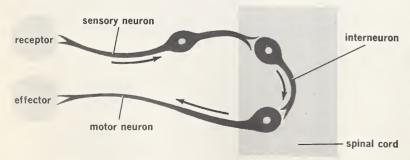
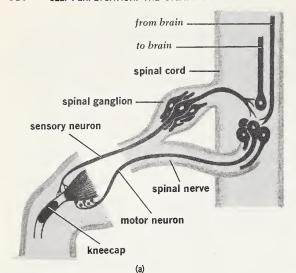


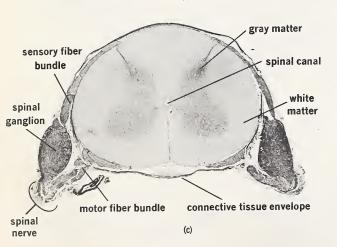
FIG. 18.2. The pattern and the components of a reflex arc. Note that neurons are not joined anatomically, but make functional connection across microscopic spaces called synapses. Note also that the cell body of the sensory neuron lies outside the spinal cord, in a so-called ganglion; that the entire interneuron lies within the spinal cord; and that the cell body of the motor neuron also lies within the spinal cord. Sensory fibers always enter the spinal cord dorsally; motor fibers always leave the cord ventrally.

THE NERVES OF THE CENTRAL NERVOUS SYSTEM

	Name	Type	Innervation
cerebrum	/ 1. Olfactory	Sensory	From nose
Celebram	2. Optic	Sensory	From eye
(5)(n)(2)	3. Oculomotor	Motor	To muscles of eyeball
	✓ 4. Trochlear	Motor	To muscles of eyeball
() () () ()	✓ 5. Trigeminal	Mixed	From and to face, teeth
1200	- 6. Abducens	Motor	To muscles of eyeball
	7. Facial	Mixed	From taste buds to salivary glands and facial muscles
0000	➤ 8. Auditory	Sensory	From ear
medulla oblongata	9. Glossopharyngeal	Mixed	From and to pharynx, from taste buds to salivary glands
cerebellum	10. Vagus	Mixed	From and to chest and abdomen
spinal cord	11. Spinal accessory	Motor	To shoulder muscles
10 0	12. Hypoglossal	Motor	To tongue
	Spinal nerves (31 pairs)	Mixed	From and to muscles in arms, legs, and trunk

FIG. 18.3. Diagram of the underside of brain and anterior part of spinal cord, showing the origin of the cranial nerves and a few of the spinal nerves. The names and functions of these nerves are given in the accompanying tabulation.





sensory neuron has its cell body just outside the brain or spinal cord, in a thickened region called a ganglion. A sensory neuron generally possesses two fibers, one leading from a receptor organ to the cell body within the ganglion, and a second fiber connecting the cell body with the interior of brain or

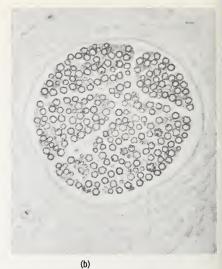


FIG. 18.4. (a) A reflex arc in the central nervous system. The knee-jerk reflex is illustrated. (b) The structure of a nerve in cross section. Note that each nerve fiber is enveloped by a myelin sheath (the dark rings). (c) Cross section through mammalian spinal cord. Note the spinal nerves, each dividing into two fiber bundles. The motor bundle connects with the cord ventrally, and the sensory bundle passes through a spinal ganglion and connects with the cord dorsally. The cord itself is a dense meshwork of neurons, the cell bodies of which are aggregated around the center, forming so-called gray matter. The axons and dendrites of these neurons are collected around the gray matter, forming white matter. The central spinal canal contains lymphilke spinal fluid. [(b) Courtesy of Dr. Mac. V. Edds, Brown University; (c) Ward's Natural Science Establishment, Inc.]

spinal cord. All the sensory neurons of a given nerve have their cell bodies in the same ganglion. Thus there are 31 pairs of spinal nerves in the c.n.s., as noted, and the sensory neurons of these mixed nerves form 31 pairs of so-called spinal ganglia (Fig. 18.4). Motor neurons of the c.n.s. do not form ganglia. Instead, their cell bodies are embedded within brain or spinal cord, and only their axon fibers project to the outside.

In the a.n.s., the sensory neurons pass through ganglia too. Indeed, the cell bodies of a.n.s. sensory neurons lie in the same 31 pairs of spinal ganglia just mentioned above. The motor neurons of the a.n.s. are arranged in a distinct pattern of their own. This pattern is determined by the arrangement of the a.n.s. centers in brain and spinal cord.

A.n.s. motor paths. In brain and spinal cord the centers of the a.n.s. are organized into two separate sets (Fig. 18.5). One set, located in the middle part of the spinal cord, represents the so-called sympathetic portion of the a.n.s. The other set, called the parasympathetic portion, is located both above and below the sympathetic portion. The upper parasympathetic centers thus reach into the brain, and we may note that all a.n.s. centers present in the brain belong to the parasympathetic system.

A given internal organ which is controlled by the a.n.s. receives motor fibers both from some part of the sympathetic system and from some part of the parasympathetic system. Therefore every such organ is regulated from two control centers. One of these two centers stimulates the organ, the other inhibits it. In some cases, the stimulating center is in the sympathetic system; in other cases, it is in the parasympathetic system. For example, the center which accelerates the heart is sympathetic, and the center which slows the heart is parasympathetic. This dual motor innervation of a.n.s.-controlled organs permits efficient adjustment of steady state. For the net activity of such organs is a resultant of a given degree of stimulation or acceleration by one set of motor nerves and a given degree of inhibition or deceleration by another set of motor nerves. The a.n.s. motor controls of a number of other organs are illustrated in Fig. 18.6.

This figure also shows that the motor paths of the sympathetic system usually are made up not of single neurons, but of at least two neurons each, one following the other. The first motor neuron leaves the sympathetic portion of the spinal cord and may terminate just outside the cord in a ganglion, one of the so-called sympathetic chain gan-

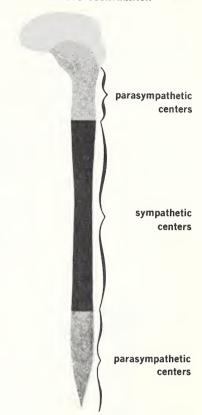


FIG. 18.5. Diagram showing the location of sympathetic and parasympathetic a.n.s. centers in brain and spinal cord. Each subdivision receives its own sensory nerves and sends out its own motor nerves. A given a.n.s.-controlled organ therefore is innervated by two sets of motor nerves, one originating in sympathetic centers, the other in parasympathetic centers.

glia. These a.n.s. ganglia form two chains, one along each side of the spinal cord. Many sympathetic motor neurons from the spinal cord terminate in these ganglia and synapse here with a second set of motor neurons (e.g., the sympathetic path to the heart). In other cases, the first sympathetic motor neurons do not terminate in the chain ganglia but

extend farther, to other ganglia located in various parts of the body. Second motor fibers then originate there (e.g., the sympathetic paths to stomach and intestine).

The motor paths of the parasympathetic system do not lead through the sympathetic chain ganglia. But they do travel through other ganglia, present along the way to given organs (Fig. 18.6).

In this connection, it is customary to refer to the first set of motor fibers, from spinal cord to a.n.s. ganglia, as preganglionic fibers, and to the second motor fibers, from the a.n.s. ganglia to the organs, as postganglionic fibers.

C.n.s.-a.n.s. interrelations. Although the c.n.s. and the a.n.s. each possess their own reflex pathways and centers, these two subdivisions of the nervous system nevertheless are interrelated both anatom-

ically and functionally. The anatomical interrelation is indicated, as noted above, by the presence of both c.n.s. and a.n.s. centers in the same brain and spinal cord and by the presence of both c.n.s. and a.n.s. sensory cell bodies in the same spinal ganglia. Also, nerve fibers of the c.n.s. and the a.n.s. often travel together within the same nerve trunk. For example, the parasympathetic a.n.s. motor fibers to the heart are situated within the trunk line of the vagus nerve, which otherwise contains nerve fibers of the c.n.s. (and is actually listed as a cranial nerve of the c.n.s.).

The close functional interconnection between c.n.s. and a.n.s. is borne out by many familiar observations. For example, visual experiences, which are c.n.s.-controlled and voluntary, may affect heart rate, which is a.n.s.-controlled and involuntary. A frightening sight may initiate a c.n.s. reflex from

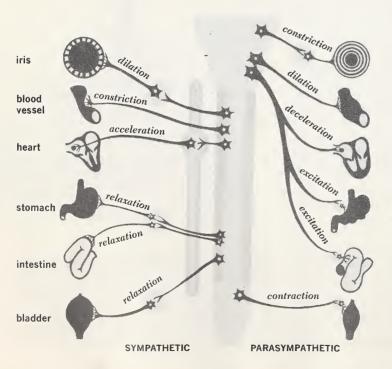
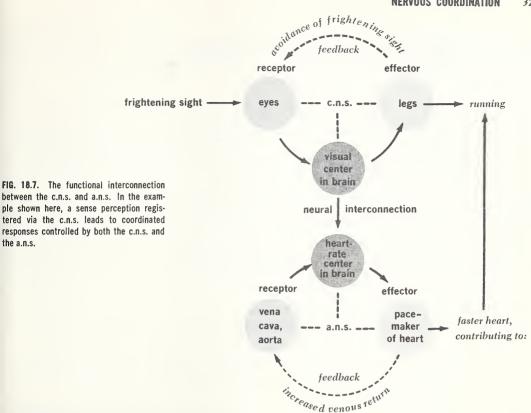


FIG. 18.6. Some of the motor pathways of the autonomic nervous system. Column to the left of spinal cord represents sympathetic chain ganglia. Each neural path shown occurs pairwise, one on the left and one on the right of the body. Similarly sympathetic chain ganglia occur both to the left and to the right of the spinal cord. For simplicity, however, only one side is indicated in each case.



the eyes to the visual center in the brain and from there to the muscles of the legs. This might lead to running and to deliberate, conscious avoidance of the frightening sight. At the same time, heart rate increases and blood pressure rises. Evidently, impulses coming into the visual center from the eyes are relayed also via interneurons to the heart-rate center. It is this kind of interconnection between c.n.s. and a.n.s. centers which produces an adaptive total response. For voluntary running could not be long sustained without an appropriate involuntary adjustment of the body circulation (Fig. 18.7). We may note, in general, that a.n.s. and c.n.s. are geared

the a.n.s.

together so intimately that any reflex in one system is likely to initiate one or more concurrent reflexes in the other.

The above outlines the basic arrangement of the neural pathways. How do these pathways function-what is a nerve impulse and how is such an impulse transmitted?

Nerve impulses

The precise nature of a nerve impulse is still unknown. We may say, in general, that an impulse is a sequence of metabolic reactions propagated along a nerve fiber. After an impulse has passed, the

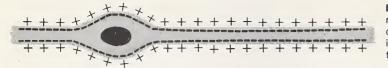


FIG. 18.8. The polarization of an inactive resting neuron. The positive charges on the outside and the negative charges on the inside produce an electric potential across the cell membrane.

reaction balance returns to the original state, readying the fiber for a new impulse. These processes consume oxygen and energy.

Accompanying the chemical changes are electrical phenomena. Indeed, the intriguing resemblance of the nervous system to a meshwork of electrical wires conducting electric currents has been the basis of many attempts to explain nervous activity. Moreover, just as one can measure currents in wires by galvanometers, voltmeters, ammeters, and the like, so this same electrical equipment can be used on nerves. But nerve impulses are not simply electrical impulses. The latter travel some 100,000 miles per sec in a wire, the former about 100 yd per sec in a nerve fiber. Nerve impulses are neither purely electrical nor purely chemical, and at present they may best be described as *electrochemical* events.

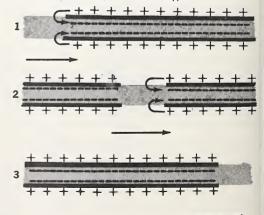
Fiber transmission. Under normal conditions within the body, stimulation of a neuron occurs at a dendrite terminal, and an impulse then travels through the cell body to an axon terminal.

Whatever else an impulse may be, it is known that it is a wave of electrical depolarization sweeping along a nerve fiber. It can be shown that a resting, nonstimulated neuron is electrically positive along the outer side of its surface membrane and electrically negative along the inner side (Fig. 18.8). These electric charges are carried by inorganic ions, attached to the two sides of the neuron membrane. As a result, an *electric potential* is maintained across the cell membrane, and the membrane is said to be polarized electrically.

Polarization, and indeed the integrity of a neuron membrane, appear to depend on *semipermeability*: the membrane is so constructed that it prevents the positive and negative ions from coming together. If semipermeability were destroyed, the membrane would depolarize; that is, the positive and negative ions would join. Conversely, if depolarization were to occur, membrane semipermeability would be abolished.

When a nerve impulse sweeps along a nerve fiber, local depolarization and simultaneous destruction of semipermeability actually do occur at successive points of the fiber membrane. As this happens at any one point, an avenue is created through which positive and negative ions of an adjacent point may meet (Fig. 18.9). In other words, the impulse itself produces the necessary conditions which allow it

FIG. 18.9. The passage of an impulse through a nerve fiber produces a local depolarization and destruction of the permeability properties of the fiber membrane, propagated in a wavelike manner through successive portions of the fiber. After an impulse has passed a given region, the original polarization and membrane characteristics reappear.



to advance farther. In this manner, it travels wavelike along a fiber. Some short time after an impulse has passed a given point, the membrane at that point recovers; that is, both the polarization and the semipermeability are restored.

Synaptic transmission. What happens when an impulse reaches an axon terminal? How does it jump across the gap of the synapse to the dendrite terminal of a neighboring neuron?

Synaptic transmission appears to be a chemical process. In certain cases, it can be shown that when an impulse reaches an axon terminal, the terminal acts like a miniature endocrine gland; it secretes minute amounts of a hormone. This hormone diffuses through the synaptic gap, some of it eventually reaches dendrite terminals of adjacent neurons, and the hormone here affects a dendrite in such a way that a new impulse is initiated in it (Fig. 18.10).

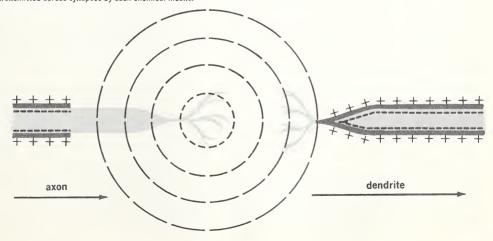
Two different hormones are known to play a role in synaptic transmission. One is adrenalin, or a substance very similar to adrenalin in chemical structure and biological effect. This hormone is secreted by the axon terminals of the postganglionic fibers of the sympathetic a.n.s. Because they produce adrenalin, these fibers are often said to be adrenergic.

The preganglionic fibers of the sympathetic system, all fibers of the parasympathetic system, and possibly the nerve fibers of the c.n.s. secrete a second type of hormone, namely, acetylcholine. Like adrenalin, acetylcholine brings about impulse transmission across neural synapses. Acetylcholine secreting fibers are said to be cholinergic.

The consequences of synaptic impulse transmission by chemicals are far-reaching. For example, diffusion takes much longer than impulse conduction within a fiber. Hence a complete reflex, involving many synapses, lasts longer than would be expected on the basis of impulse speeds within fibers alone. Being "slow on the uptake" is largely a result of delays at synapses.

We may note too that nerve fibers as such rarely fatigue but synapses get tired easily. When they are operating intensely, axon terminals may temporarily exhaust their hormone-secreting capacity,

FIG. 18.10. Diagram of a neural synapse, showing the release and local spreading of hormones from the axon terminal of one fiber to the dendrite terminal of another. Impulses are transmitted across synapses by such chemical means.



and synaptic transmission then slows even more or stops altogether for the time being.

Finally, we may note that synapses impose a one-way direction on neural pathways. A nerve fiber can be stimulated artificially at either end or in the middle, and impulses then travel backward, forward, or in both directions. But only axon terminals are specialized to secrete hormones, and only dendrite terminals are sensitive to these hormones. Hence the unidirectional conduction of impulses.

The first nerve impulse in a reflex arc is normally produced by a sensory receptor organ. Such organs begin all nervous activity, and on their functioning depend all subsequent neural events. How are receptors constructed, and how do they work?

THE NEURAL RECEPTORS

330

We do not see with our eyes and do not hear with our ears. Nor do we see or hear with our brain. Seeing, hearing, "sensing" in general require the operational integrity of a sensory receptor and of a sensory neural path and of a neural center, which interprets the signals received.

Mammals possess many more than the familiar five senses of vision, hearing, smell, taste, and touch. They also sense pain, pressure, heat, and cold. They sense the position of their limbs, the mechanical equilibrium of their bodies, and the motion of their bodies, all without looking. They possess a genital sense, and they experience distinct sensations when tickled, when a limb "falls asleep," when the skin "stings" or "burns," when they are hungry, thirsty, or sleepy. These are only some of the numerous senses which penetrate into the conscious. And in probably more than an equivalent number of senses, conscious awareness is lacking. For when a blood vessel dilates under pressure, sensing is involved also.

A separate type of receptor structure probably does not exist for each of these senses. Only about a dozen different kinds of receptors are demonstrable. They mediate different sensations when stimulated singly and when a varied group of them is stimulated together. Receptors are often classified as exteroceptors and interoceptors, i.e., structures receiving information either about the outside world or about the interior of the body. All are alike in that they translate specific stimulus energies into specific nerve impulses.

We first discuss receptor types distributed widely throughout the body.

Dispersed receptors

Structural types. The simplest type of neural receptor is a free nerve ending. The hairlike dendrite terminals of sensory neurons may carry a series of nodular thickenings or may be bunched together like balls of twine, but beyond such structures other functional parts are not present. This is probably the most widespread kind of neural receptor. Relatively simple sensory endings of this sort relay a.n.s. signals from many internal organs, as well as a large variety of c.n.s. signals. For example, muscle sense and tendon sense (by which we feel the position of body parts) and the sense of pain are mediated by plain or variously nodulated and coiled sensory endings (Fig. 18.11).

Moreover, comparatively simple nerve endings represent one type of receptor for touch stimuli. Each hair in the skin is surrounded at its base by a net, or plexus, of sensory fiber terminals (Fig. 18.11). When a hair is bent, the position of the hair base changes slightly, and this stimulates the fiber plexus. The resulting nerve impulses are interpreted as touch.

Touch stimuli are received additionally by sense organs located in the skin. These are tiny structures made up of many specialized cells (not neurons), innervated by sensory fiber terminals (Fig. 18.11). Here it is the organ, not the fiber terminal, which translates stimulus energies into nerve impulses. Touch organs may be clustered together relatively densely, as in finger tips, palms, and lips, or they may occur sparsely, as on the back.

In addition to touch organs, the skin also contains tiny organs sensitive to heat, to cold, and to

FIG. 18.11. Some types of neural receptors in the skin. (a) Free nerve ending (pain). (b) Nerve plexus surrounding hair (touch). (c) Pacinian corpuscle (pressure). (d) Organ of Ruffini (pressure). (e) Organ of Krause (cold). (f) End organ of Ruffini (warmth). (g) Meissner's corpuscle (touch).

pressure. Together with the numerous touch organs and pain fibers in the skin, these make up what are called cutaneous receptors. They vary in relative distribution and in number. It is estimated that the human skin contains some 4 million pain receptors, 1/2 million pressure receptors, 150,000 cold receptors, and 16,000 heat receptors.

Functional properties. Very little is known about the mechanism by which specific stimuli, affecting either the tiny organs or free nerve endings, produce nerve impulses. In all probability, stimulus reception is brought about primarily by environmental change as such. For when the altered situation persists unchanged for a time, a sense dulls, or "adapts." For example, we soon become relatively insensitive to the pressure of clothes, a persistent odor, or a taste. Ease of adaptation varies, pain probably being most difficult to adapt to. On the

other hand, odor perception dulls very easily. We cannot judge our own body odors, for example. We live with them constantly, and we are continuously adapted to them.

Sensations depend on stimulation of appropriate receptors. For example, the feeling of pressure is contingent on impulses emanating from pressure points; only pressure receptors are able to register pressure stimuli. A complex stimulus may affect more than one kind of receptor, in which case a composite sensation is perceived. For example, simultaneous impulses from heat and pain receptors may give rise to a burning sensation. Similarly, when one enters a hot shower, both hot and cold receptors may be affected and one may feel hot and cold at the same time. Ice on the skin may produce sensations of burning, through simultaneous stimulation of cold, heat, and pain points.

It can be shown dramatically that the different

kinds of sense perceptions depend not so much on impulse differences as on the different central connections of fibers coming from various types of receptors into the brain and spinal cord. For example, it is possible to cut a fiber from a heat receptor and a fiber from a cold receptor and to let the cut ends reinnervate the sense organs, but in switched order. The fiber from the heat receptor then terminates in the cold center of the brain, and the fiber from the cold receptor terminates in the heat center. Under such conditions, the organism feels hot every time the cold receptor is stimulated and cold every time the heat receptor is stimulated. Evidently, the quality of a sensation is determined not by the receptor, nor by the type of nerve impulses sent by the receptor, but by the neural centers. The sensation depends on which of various centers receives signals.

Furthermore, correct localization of a stimulus hinges on the central connections too. If pain fibers from finger tip and big toe were switched as above, then a needle prick on the big toe would prompt immediate examination of the finger for blood, and vice versa. We may note that the anatomical distribution of receptors throughout the body is matched virtually point for point in the anatomical distribution of neural centers. Each receptor has its neural center, and so long as the structural relationships are preserved, impulses will be correctly interpreted as coming from particular body regions and particular receptors.

We may qualify this generalization in one respect. It is a fairly common experience that pain originating in an internal organ is often sensed as if it originated at some remote skin area or at another distant internal region. For example, pain stimuli actually affecting the liver may be "referred" to the shoulder region. Pain in the uterus may be erroneously thought to originate in forehead, chest, and palm of hand. Similarly, an ache in one tooth is often thought to come from the whole side of the head. In all such cases of referred pain, pain fibers originating in different body regions lead into the same general area in the brain or spinal cord. Im-

pulses arriving through one of the fibers may stimulate a greater or lesser portion of that area, as if impulses actually arrived over more than one pain fiber. As a result, pain sensations may be diffuse and may be referred to numerous body regions.

All receptor types discussed so far agree in that their distribution is body-wide. The most familiar receptors, on the other hand, are confined to specific body regions. In this category of localized receptors are the sense organs of the tongue, the nose, the eye, and the ear.

Taste and smell

The tongue. Our reduced tasting ability when the nose is blocked with a cold reveals that smell is an integral component of "taste." The receptors on the tongue are affected by chemicals in solution, and the receptors in the nasal epithelium, by vapors of chemicals. Our sensory judgment about a substance is keenest when impulses from both tongue and nose reach neural centers.

Clusters of elongated ciliated cells, set into depressions in the tongue, form taste buds (Fig. 18.12). Sensory-fiber terminals from each of the bud cells lead into the brain. Taste buds are distributed all over the upper tongue surface, and although structural differences among buds cannot be demonstrated, well-known functional differences exist; the four primary taste sensations, *sweet*, *sour*, *salty*, and *bitter*, arise through stimulation of buds at different regions of the tongue. Bitter substances primarily affect buds located at the back of the tongue; sweet substances, buds in the forward part of the tongue; and sour and salty materials are tasted predominantly along the tongue edges (Fig. 18.13).

Here, as in other sense perceptions, it is the central connections that matter. Certain chemicals exist which, when applied to the tongue tip, produce a sweet sensation, but when the same chemicals are applied at the back of the tongue, they produce a bitter taste. Evidently, chemicals to which we are sensitive do not possess "inherent" taste, but only have the property of stimulating this or that taste

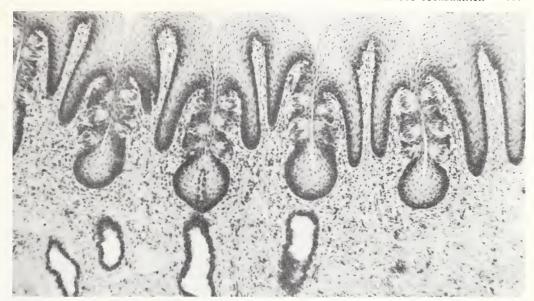


FIG. 18.12. Section through the tongue, showing taste buds. The buds are located at the ends of deep narrow channels leading into the tongue from the surface. (General Biological Supply House, Inc.)

bud. And depending on which of the tongue areas sends impulses to its unique brain connections, a given subjective taste sensation will be registered.

Therefore, to say that "Sugar is sweet" erroneously implies an objective sensation, and the only pertinent objective property of sugar is its capacity to stimulate certain taste buds. In different individuals, one and the same sugar may produce qualitatively and quantitatively different sensations of sweetness. At least one substance is known which one person may not taste at all, but which might taste sweet to another, bitter to a third, salty to a fourth, and sour to a fifth. This substance is *phenyl*thiocarbamide. Individually different reactions of this sort trace back to differences in heredity.

Taste buds are highly sensitive receptors. Quinine for example, a substance normally producing a bitter taste, generally can be sensed in concen-

trations as low as 1 part in 2 or 3 million parts of water.

A large variety of composite tastes are built up from different combinations and intensities of the four basic tastes, from smell, and from other sense perceptions initiated in the mouth. For example, both a hot meal and a cold meal affect the same taste buds if the two meals are alike chemically. But the hot meal vaporizes more, hence smells more, and it also stimulates heat receptors in the lining of the mouth and on the tongue. The hot and the cold meals consequently taste different.

The nose. Varied as taste sensations are, odor perceptions are even more diversified. Attempts to establish basic odors, from which all others can be derived, have met with relatively little success. A fairly adequate scheme can be constructed on the

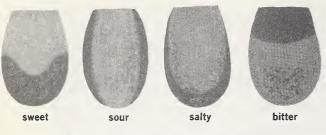


FIG. 18.13. Diagrams of the tongue, showing the distribution of taste buds for the four taste sensations.

basis of four primary odors, rancid, vinegary, fragrant, and burnt, each classified in various intensities.

Part of the ciliated lining in the upper nasal passages is the receptor tissue for the sense of smell in vertebrates. Sensory fibers lead into the olfactory lobe of the brain, relatively small in man but large in other vertebrates. Man is a comparatively poor smeller, but in most other vertebrates, the sense of smell is as well developed and has the same outstanding importance as vision in man.

As among taste buds, structural differences among the cells of the nasal epithelium cannot be detected. Moreover, it is virtually impossible to determine which receptor cells in the nose mediate perception of what odors. Are there as many functionally different types of receptor cells and central fiber connections as there are different odors? Probably not. Is each receptor cell capable of emitting as many different types of impulses as there are different odors? Again, probably not. When the perception of one odor dulls by adaptation, perception of other odors is usually not dulled. This suggests that functionally distinct receptor cells and central connections do exist to some extent, each receptor cell perhaps being able to emit different impulses for a small group of different odors. Paradoxically, our understanding of smelling mechanisms is much less satisfactory than that of the manifestly more complex visual and auditory mechanisms.

Vision

The human eye is among the most efficient light receptors developed during evolution. Insect eyes possibly are better adapted for the detection of motion, and many birds may focus on five horizon points at once without moving their heads. But the human visual apparatus probably registers color more clearly than that of any other animal, and human eyes are virtually as sensitive as eyes can possibly get; two or three photons suffice to stimulate, a photon being the smallest unit of light.

The eye. The eye is made up of three coats (Fig. 18.14): an outer sclera, fibrous in man, cartilaginous in many other mammals; a middle choroid, a layer which is pigmented black and which carries blood vessels to and from the eye; and an inner retina, the actual light-receptor tissue. In many mammals, a thin film of whitish-greenish crystalline material coats the choroid layer. This material reflects light, and in the dark it makes the eyes of these animals shine and glow.

In the front part of the eye, the three coats are modified structurally. The sclera merges into the transparent cornea. The choroid coat continues as the sometimes pigmented iris, which encloses the pupil, and as a ring-shaped muscle, the ciliary body, to which the lens is attached by ligaments. The spaces between lens and cornea are filled with the fluid, lymphlike aqueous humor, and the space between lens and retina contains a glassy, jellylike material, the vitreous humor.

Functionally, the eye resembles a photographic camera, with one major difference. A camera is focused by varying the distance between lens and film. The eye is focused by adjustment of the curvature of the lens, the lens-retina distance remaining fixed (Fig. 18.15). A beam of light passes through the cornea, through the pupil, into the lens. The pupillary opening corresponds to the diaphragm of a camera; it enlarges or becomes smaller, regulating the amount of light admitted into the eye. This control mechanism is set into operation by light itself.

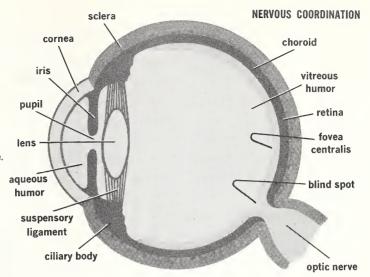
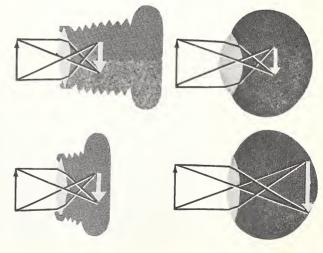


FIG. 18.14. The structure of the eye.

Intense light initiates a reflex via retina, the autonomic nervous system, and a set of circularly arranged muscles in the iris. These muscles contract, and the pupil becomes smaller. Conversely, low light intensity reflexly produces contraction of a set of iris muscles arranged like the spokes of a wheel, and the pupil of the eye then enlarges (Fig. 18.6).

The lens focuses an object onto the retina. When a far-off object is viewed, and when the eye is at rest, the lens is fairly flat. As an object moves nearer, the lens curves out increasingly (Fig. 18.16). Lens shape is controlled by the ciliary body. When this muscular ring is relaxed, the ligaments holding the lens are taut and the lens is flat. Conversely, when the ciliary muscle contracts, the lens ligaments relax and the lens, an elastic structure, is then allowed to curve out. The ciliary muscle is under reflex control. A blurred image on the retina elicits reflex impulses to the ciliary body, which contract or relax that body more, until the image is no longer blurred. The adjustment reflex then ceases, and a focused image so reaches the retina. Note that the image of an object is projected on the retina in an inverted position.

FIG. 18.15. Focusing in camera and in eye. Upper figures: images fall short of photographic film and retina. Lower figures: camera is focused by changing the lens-film distance, and eye is focused by changing the curvature of the lens.



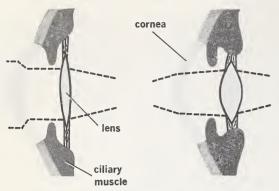


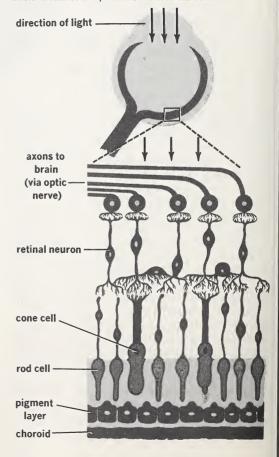
FIG. 18.16. Focusing when object changes distance. Left: far object, flat lens. Right: near object, curved lens. Lens curves out when the muscles of the ciliary body contract.

The retina. This tissue is made up of several layers of neurons and of one layer of rods and cones. These are the receptor cells which translate light energy into nerve impulses (Fig. 18.17). Note that the rod-and-cone layer is adjacent to the choroid coat. Hence light must pass through the neuron layers before it reaches the rods and cones. These light-receiving cells connect functionally with the neurons of the retina. The neurons synapse among one another in intricate ways, and nerve fibers from the whole inner surface of the retina eventually collect in one region and form the optic nerve to the brain. Where this nerve leaves the eye, somewhat off center, it interrupts the continuity of the rod-and-cone layer and of the choroid and sclera. This is the blind spot, so called since visual images cannot be formed at this point.

Rods and cones are distributed unevenly in the retina. In the center of the retina is a tiny depression, called the **fovea** centralis (Fig. 18.14). In this area only cones occur. Neurons are absent here, and the cones are exposed to light directly. Cones are responsible for color vision and for the perception of sharp, bright images. Indeed, the fovea is the area of most acute vision. Cones are distributed less densely through other parts of the retina, and at the

retinal periphery cones do not occur at all. Rods, on the other hand, are particularly abundant here. Rods are sensitive to dim light, and they serve predominantly in the detection of motion; we notice a moving object well when we view it out of the corners of our eyes. Away from the retinal periph-

FIG. 18.17. Diagram of the retina in section, greatly simplified. Note that the neuron layers of the retina are toward the inside of the eye and that light must pass through these layers before it reaches the photosensitive rods and cones.



ery, rods are distributed more sparsely, and they are not present at all in the fovea centralis.

The chemical basis of light reception in rods is relatively well known. Rod cells contain a photosensitive pigment called visual purple. When light strikes it, the pigment is bleached through a photochemical reaction, and two endproducts are formed. One is a substance called retinene, which is linked to a protein fraction. The other endproduct is energy, which stimulates an optic neuron and produces a nerve impulse (Fig. 18.18). In the dark, and with the aid of respiratory energy, the retineneprotein complex may be reconverted into visual purple. Alternatively, retinene protein may first be transformed into a vitamin-A-protein complex, which may regenerate visual purple in turn. In very intense light, visual purple may be destroyed faster than it can be formed. Vision then may become impaired (e.g., snow blindness). We may also appreciate how vitamin-A deficiency would interfere with vision.

Light-initiated chemical reactions which produce impulses take place in cone cells too, but processes here are understood less well. The photosensitive pigment iodopsin is known to be present in cone cells. Are there different cones for each color? Probably not. Any color, including white, can be produced from various combinations and intensities of three primary colors, namely, red, green, and blue. Most theories of color vision presuppose that

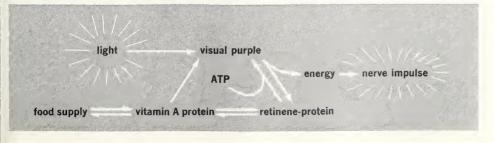
three functionally different cone types exist, one for each primary color. Indeed, color television is based on an analogous principle.

Impulse interpretation. An external object is "pictured" on the retina as a series of points, like the points of a newspaper photograph. Each point corresponds to a rod or a cone. Impulses from these points are transmitted into the brain according to the following pattern.

All fibers from the left sides of both eyes lead into the left half of the brain; and all fibers from the right sides of both eyes lead into the right half of the brain (Fig. 18.19). In each brain hemisphere there is a circumscribed region, the optic lobe, where fiber tracts from the eyes make synaptic connections with the neurons of visual centers. It can be shown that for each group of rods and cones there exists a corresponding group of interpreter neurons in the optic lobes. In other words, the "point picture" of an object on the retina is duplicated more or less faithfully in the optic lobes, by impulses from specific rods and cones to their correlated interpreter neurons. Stimulation of the latter registers as vision.

It should be clear that the left half of every external field of vision produces images in the right halves of both eyes. Similarly, the right half of what can be seen is focused onto the left halves of both retinas (Fig. 18.19). Therefore, in view of the

FIG. 18.18. The pattern of the chemistry of rod vision. Note that visual purple may be regenerated either from the retinene protein or from vitamin-A protein.



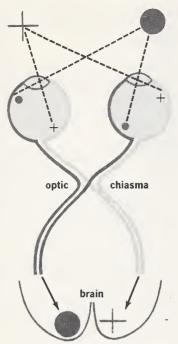


FIG. 18.19. The nerve fiber tracts from eye to brain. An object in the left field of vision registers on the right halves of both retinas, and impulses are transmitted into the right half of the brain.

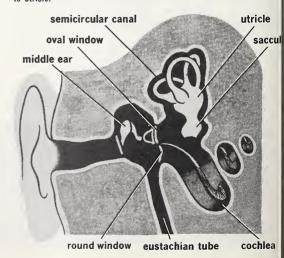
fiber patterns from eyes to brain, the right half of a field of vision registers in the left half of the brain and the left half of vision field registers in the right half of the brain. The left and right optic lobes are not directly continuous. Yet interpreter activity normally is such that the "left" picture of the external world is joined smoothly to the "right" picture. Moreover, both halves of the picture are sensed right side up, even though the retinas receive inverted images. Left and right pictures sometimes fail to join smoothly, as under the influence of alcohol, in which case one "sees double."

Why is an inverted retinal image not also "seen" as an inverted picture? The answer is that the optic

centers in the brain have learned to give visual experiences correct orientations. Our recognition of up, down, and sideways is based ultimately on sensing the direction of gravitational pull. Muscles and ears play an important role in this, as the next section will show. Hence, even if we imagined that retinal images actually arrived in the optic lobes in an inverted position, gravity perception would teach us, shortly after birth, to associate the bottom part of a picture with the idea of "up," the upper part with the idea of "down." In outer space there would be no such gravity orientation and any visual or gravitational notions of "right-side-upness" would would become meaningless.

How does an impulse arriving in an optic neuron in the brain produce a conscious sensation of light? How indeed does any other sense become conscious? Answers to this cannot be given as yet. However, it is known that an immense number of more or less direct neural paths lead from vision-interpreting centers to virtually all other centers in the brain and spinal cord. Consequently, a tremendous num-

FIG. 18.20. The gross structure of the ear. Note ear bones in the middle-ear cavity and attachment of semicircular canals to utricle.



ber of reflexes can be initiated through the receptor cells in the eyes, and it is this which makes the sense of vision so important to man.

The ear

This organ houses receptors for three senses: the sense of static body balance, the sense of dynamic body balance, and the sense of hearing.

The outer ear carries sound to the eardrum, a membrane which separates the cavity of the middle ear from the outside (Fig. 18.20). The connection of this cavity with the mouth via the eustachian tube has already been referred to (Chap. 12). Three tiny middle-ear bones, hammer, anvil, and stirrup, moved by the smallest muscles in the body, form an adjustable bridge from the eardrum, across the middle-ear cavity, to the inner ear. The latter is an intricate system of canals and spaces, surrounded by bone and filled with lymphlike fluid. These chambers are closed off from the middle ear by two membranes. One is stretched across a so-called round window, and one across an oval window. The stirrup bone of the middle ear is anchored to the membrane of the oval window.

The inner ear consists of three functional and structural divisions: a chamber consisting of two parts, the utricle and the saccule; the semicircular canals; and the cochlea, a structure coiled like a snail shell. These tunnels and cavities are interconnected.

Balance. The receptors for static body balance are located in the utricle and saccule. At several places along the walls of the chambers, there are clusters of specialized cells. Sensory nerve fibers lead off from one side of these cells, and tiny hairs project from the other. The tips of the hairs of such a cell cluster attach to a tiny ear stone, a calcium-containing body (Fig. 18.21). When the stone is in a certain position, it pulls on some of the hairs more than on others, and this stimulates the cells to which the hairs are connected. Nerve impulses from these hair cells to the brain register the particular position of the ear stone. When the head is tilted,

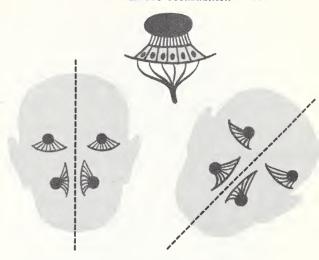


FIG. 18.21. Upper figure: a receptor organ for static balance, showing hair cells and ear stone (diagrammatic). Lower figures: position of the receptor organs in relation to the head and the effect of tilting the head.

or when the balance of the body as a whole is changed, then gravity acts on all the ear stones and shifts them in a given manner. This pulls different sets of hair cells, and different sets of impulses to the brain inform of the change in balance. Reflex signals from the brain then ensure that equilibrium is not lost.

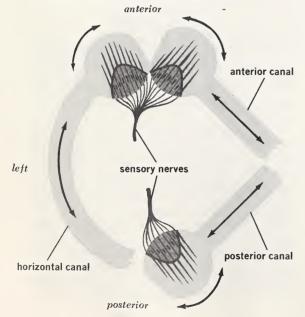
This sense permits recognition of up, down, side, front, and back, even when visual stimuli and sensory impulses from muscles fail to provide such recognition. A blindfolded mammal with inoperative ear-stone mechanisms has difficulty in remaining upright; and when its position is abnormal, it does little to correct this position.

The sense of movement and of dynamic body balance is mediated by the semicircular canals. There are three in each ear, looping from the utricle back to the utricle. The canals are placed at right angles to one another, in the three planes of space (Fig. 18.20). At one end of each canal is an enlarged

portion, and in it is found a cluster of hair cells, rather similar to those described above. However, there is no ear stone and the hairs are longer.

When the head is moved, the semicircular canals move with the head. But the fluid in the canals "stays behind" temporarily, as a result of its inertia, and "catches up" with the head only after the head has stopped moving. This lag in fluid motion bends the hairs of the receptor cells, producing nerve impulses. Depending on the direction and intensity of fluid motion in the three pairs of canals, different impulse patterns are transmitted to the brain. Every straight-line motion or rotation of the

FIG. 18.22. The semicircular canals of the left ear. The top of the diagram is anterior, and the right side is toward the mid-plane of the head. The three canals are set at right angles to one another, and therefore only the horizontal canal reveals its curvature in such a view. Both ends of each canal open into the utricle. One end of each canal is enlarged into a chamber, and in it are present the hair cells which function as receptors for the sense of dynamic balance. Arrows indicate motion of internal fluid when the head is moved.



head, or of the body as a whole, produces a distinct impulse pattern, hence a distinct sense perception (Fig. 18.22).

Mammals, which pursue a more or less twodimensional way of life, are relatively unaccustomed to up-and-down motion. Indeed, such motion initiates reflexes via the semicircular canals leading to well-known symptoms of dizziness, nausea, and gastric upsets. Seasickness is produced in this way, as is the discomfort experienced when one rides in an elevator. Lying flat on a ship, or bending one's head in an elevator, reduces the upsetting sensations, since the head is then in the same relative position to the direction of motion as in walking. The sense of balance may also be affected by rapid temperature change in the environment. For uneven cooling or warming of the fluid in the semicircular canals may produce currents which may stimulate the receptor cells. Sensations of motion or of dizziness may then be experienced, even if the head does not move.

Hearing. The functioning of the cochlea as the receptor for the sense of hearing is understood fairly well today. The internal space of the cochlea is partitioned into canals by membranes running the length of the cochlear coils. One of these membranes, the basilar membrane, supports rows of hair cells, the actual receptors (Fig. 18.23). Nerve fibers lead from them to the brain. The hairs make contact with the tectorial membrane, a fold of tissue which overhangs the receptor cells. Basilar membrane, hair cells, and tectorial membrane together constitute what is called the organ of Corti.

Sound waves set the eardrum into vibration. This motion is communicated via the middle-ear bones to the oval window. As the membrane at this window vibrates, it sets the fluid of the inner ear into vibration also. Since fluid is practically incompressible, the membrane over the round window bulges outward every time the membrane over the oval window bulges inward, and vice versa. The round window thus serves as a pressure compensator.

The fluid of the inner ear, including the cochlear

fluid, now vibrates in harmony with external sound waves. What takes place next involves the basilar membrane particularly. This membrane contains strands of tough connective-tissue fibers, stretched transversely across the cochlear tube. At the base of the cochlear coil these fibers are shortest, and at the tip of the coil they are longest. The fibers may vibrate at different rates or frequencies according to their different lengths. In this respect they resemble the tone strings of a piano.

These basilar fibers are set into vibration by the cochlear fluid. As the fluid vibrates at a given frequency under the impact of external sound waves, it sets into motion those basilar fibers which vibrate at the same frequency. This is a selective *resonance* effect. In a similar way, a string of a piano may be set into resonating vibrations if a corresponding sound is produced nearby with a tuning fork, for example, or by striking an appropriate key on another piano.

In the ear, therefore, different external sound patterns first produce different vibration patterns in the cochlear fluid. This in turn then produces vibrations in particular sets of basilar fibers. As a result, the hair cells attached to the vibrating basilar fibers move up and down. And as these cells touch against the overhanging tectorial membrane, their hairs are bent and nerve impulses are initiated. Each different sound pattern thus gives rise to a different pattern of nerve impulses.

The impulses are transmitted via the auditory nerves into the temporal lobes of the brain, where the hearing centers are located. Here the nerve fibers from the hair cells in the cochlea make individual connection with separate neurons, and each of these interprets a different pitch. For example, a high-frequency sound wave selectively produces nerve impulses in hair cells attached to the short basilar fibers, and the particular neurons in the hearing center which receive these impulses interpret them as a highly-pitched sound. If these portions of the hearing centers should be injured, deafness to high sounds would result. Analogously, selective deafness to low sounds is known to occur.

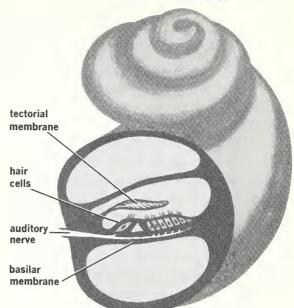


FIG. 18.23. The cochlea (diagrammatic). Note the coils of the cochlea and the cochlear cross section showing the parts of the organ of Corti.

Although animals such as dogs hear a wider range of sounds and are probably more sensitive to sound than man, the ear of man is unsurpassed in distinguishing tones of only slightly different pitch and tones of widely different quality. As an interpretive sense, and as an important adjuster of speech, hearing has acquired a human importance second only to vision.

THE NEURAL CENTERS

Structural features

The brain and the spinal cord consist of dense, exceedingly complexly organized accumulations of neurons. Many of these accumulations form functionally distinct "nerve centers," where given sen-

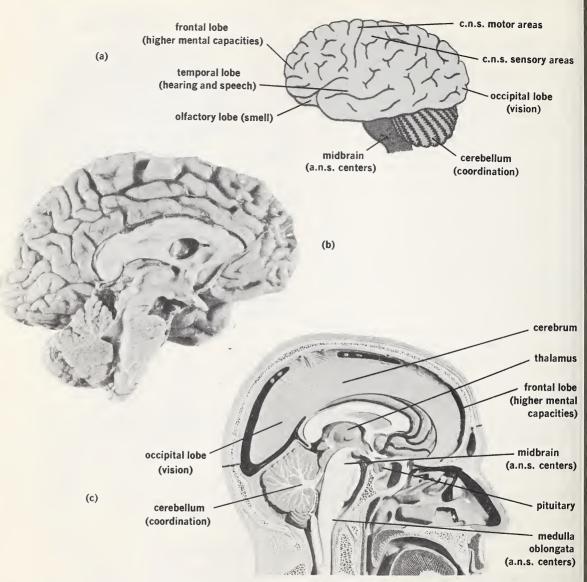


FIG. 18.24. (a) The left half of the brain, viewed from the outside. The functions of the various labeled parts are indicated in parentheses. (b) The left half of the brain, viewed from the inner cut side. The various parts and their functions are indicated in the model shown in (c). [(b) Photographic Department, Rhode Island Hospital; (c) Detail of model designed by Dr. J. F. Mueller, Ward's Natural Science Establishment, Inc.]

sory impulses are received and interpreted and where motor impulses are sent out over appropriately selected motor pathways. Other neurons in brain and spinal cord form extensive fiber tracts to and from the centers.

The specific locations and functions of many centers in brain and spinal cord have been discovered by observing the effects of accidental or experimental damage. In a newer, more precise method, selected points in brain or spinal cord may be stimulated electrically with needle electrodes. The resulting responses of a test animal may then provide clues to the control functions of the stimulated areas. By such means, distinct subdivisions in brain and spinal cord have been identified and the location of a large number of neural centers has been pinpointed.

In the brain (Fig. 18.24), the deep central portions (midbrain) and the posterior medulla oblongata contain largely a.n.s. centers. Situated dorsal to the medulla oblongata is the cerebellum, which is the chief motor coordinator. It integrates, for example, the many muscular motions involved in walking or in speaking. The cerebrum, consisting of a left and a right "hemisphere," forms the outer portions of the brain, along the top and the sides. The cerebrum contains most of the cranial c.n.s. centers. Its frontal lobe particularly is also the seat of the higher mental capacities.

The surface layers of the cerebrum are grooved and ridged conspicuously. In this cerebral cortex are located cell bodies of many neurons. The axons and dendrites of these neurons project into the deeper portions of the cerebrum, and since these fibers contain fatty myelin sheaths, they appear white when viewed in bulk. The deeper parts of the cerebrum are therefore designated as white matter, in contrast to the gray matter of the cerebral cortex, formed by the nonmyelinated cell bodies of neurons.

The arrangement is reversed in the spinal cord (Fig. 18.4). Here the gray matter, formed by non-myelinated cell bodies, is in the core, and the white matter, formed by myelinated fibers, is on the outside.

Functional features

In general terms, the functions of brain and spinal cord are of four principal kinds.

First, brain and spinal cord serve in pathway selection. Neural centers receive sensory impulses from receptors, and then they select among thousands of possible motor pathways going out to effectors. Signals are sent only to some effectors and only to appropriate effectors. As a result, the effector response of an organism to a given stimulus can be adaptively useful and can actually aid in steady-state maintenance. In all probability, the spinal cord carries out only such "switchboard" activities and none of the functions below.

Second, in addition to its role as pathway selector, the brain also serves as reflex modifier. It may suppress or exaggerate responses to incoming information, as when we decide not to cry out under pain or to cry out more than is necessary. It may store incoming information as memory and may thereby delay the completion of a reflex for shorter or longer periods. On occasion its modifying action may be unduly intensified, as in different mental diseases. Variously inappropriate effector responses are then produced.

Third, the brain is the principal coordinating center. It integrates into composite, unified sense perceptions the impulses arriving from many different receptors. And it gears together into smoothly coordinated actions the motor responses of many different effectors.

Fourth, the brain is the controller of such higher mental capacities as an animal possesses, i.e., those associated with consciousness, memory, intelligence, and personality. The significance of these capacities to mammals in general, and to man in particular, is well appreciated.

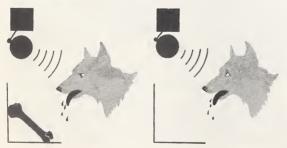
Of these control functions, pathway selection probably is the most fundamental, and all others may be based on it. How is the selection of appropriate neural pathways accomplished? At the present state of knowledge, the answer is largely unavailable. Among several tentative suggestions

and speculations, one is the idea of pathway facilitation. This notion emerges from the observation that nerve impulses often may travel more easily over some neural pathways than over others. For example, it is easier to perform a familiar activity than an unfamiliar one. From this, the hypothesis of pathway facilitation suggests that the more frequently impulses travel over given neural circuits, the less resistance this circuit may offer to subsequent impulses.

As an analogy, we may imagine the brain to be like a mass of clay, and impulses, like grooves cut into the clay. Then the more often the same groove is traveled by the cutting tool, the deeper it becomes, and the more surely will the tool be guided subsequently. Preferential selection of one neural path over others therefore might be partly a matter of having used a given path repeatedly; wherever a choice of circuits exists, the well-used, facilitated circuits may be selected in preference to the previously little used, unfacilitated ones. To be sure, it is far from clear just how a circuit in brain or spinal cord might become different, structurally and/or functionally, when it becomes facilitated.

Habit formation and learning by repetition and by trial and error become explainable in general terms on this basis. For example, in a young animal,

FIG. 18.25. The principle of conditioned reflexes. Left: two simultaneous stimuli (sight of food, sound of bell) produce a response (salivation). Right: if the procedure is repeated often, then a single stimulus alone may eventually produce the characteristic response.



few brain pathways are as yet firmly established by facilitation. Incoming impulses are transmitted more or less in all directions, and behavior is relatively uncoordinated and random. But among the random impulse paths, some will bring about advantageous effector results. The same pathway pattern may then be tried time and again, and a facilitated neural route may eventually be established.

Learning, maturing, gathering experience thus may be a matter of blazing ever new neural trails, and when new trails become old, a habit has been acquired. To be sure, many neural routes are already fully facilitated at or before birth, and these are responsible for inherited, instinctive behavior. Indeed, most animals depend almost entirely on such inborn neural circuits, and later learning and habit formation play only minor roles at best.

Facilitation may also be at the root of learning by conditioned reflex. Such reflexes have originally been demonstrated on dogs, by the Russian biologist Pavlov. When a hungry dog sights food, his saliva and gastric juice begin to flow reflexly. If, on many successive occasions, a bell is sounded every time food is presented then the flow of digestive juices can eventually be initiated by sounding the bell alone, without giving food. Evidently, the dog learns to associate the bell with food, and instead of one facilitated pathway to the digestive glands, there are now two. Either one alone, or both together, may initiate secretion (Fig. 18.25).

Neural conditioning of this sort plays a considerable role in behavior development, not only in dogs but in mammals generally, man included. And making associations of originally separate neural circuits may account for much of intelligence, for insight, for "getting the idea." Suppose that two well-facilitated pathways are established, each representing one item of information. "Seeing the connection" between such seemingly unrelated bits of information might mean the emission of impulses over a third neural pathway, interlinking the two. This might be accomplished by "speculating," i.e., by letting impulses travel more or less at random over existing paths or by trying new paths. Among

these might be found a route which all at once gives connected meaning to separate pieces of information. The more widely a person is able to correlate in this way, the more intelligent he is likely to be. This might well mean that such a person can make numerous and varied path connections in his brain—possibly because he uses his brain often enough even when he does not have to—and so facilitates a large number of neural routes among the trillions potentially available.

The net result of nervous operations as a whole is control of *muscular movement* and of *glandular secretion*.

But is it not really more than this? Conscious, contemplative thinking, reading, aesthetic appreciations, and all other higher mental functions, are they not more than mere reflex control of muscles and glands? Actually not. For all mental activity aims toward some action, potential or actual, present or future. On the one hand, we see, hear, learn, store information, correlate information; in short, we think. And on the other hand, we speak, walk, build, vote; in short, we do. All this doing requires, and is directly brought about by, muscular and glandular activity. In the final analysis, therefore, thinking sets the stage for moving muscles, and

better thinking implies more judicious use of muscles. Because muscular control contributes powerfully to the maintenance of steady states, nervous systems have become vital components of animals.

Throughout these chapters on steady state, the central running theme has been that, by virtue of its built-in hierarchy of control systems, the protoplasmic unit may attain an actual life span which approaches that potentially inherent in it. When the controls fail for any external or internal reason, disease occurs. Intact controls may then be able to restore steady state. However, in time even the best-controlled system goes out of control. As the component parts age and wear out, functional and structural breakdowns occur in so rapid a succession, and in so many different places at once, that not enough controls remain intact to make the necessary repairs. Disintegration and death must be the eventual outcome.

But, as pointed out in Chap. 3, living systems here reveal their superiority of design and construction over any nonliving system. For before final disintegration supervenes, the living controls may call into action another self-perpetuating device, one which anticipates even the powerful stimulus of death: reproduction.

REVIEW QUESTIONS

- 1. Describe the structure of a neuron. How do neurons in c.n.s. and a.n.s. differ structurally and functionally? Describe the components and the arrangement of a reflex arc. Distinguish between nerve fibers and nerves. What different kinds of each are known?
- 2. Describe the organization of the c.n.s., its nerves, and its centers. Review the course of a c.n.s. reflex arc. What is a ganglion?
- 3. Describe the organization of the a.n.s., its nerves, and its centers. What are the (a) structural, (b) functional differences between the sympathetic and the parasympathetic systems? What are sympathetic chain ganglia?
- 4. What are preganglionic and postganglionic fibers? Describe the course of an a.n.s. reflex arc. Review the

- innervation of the heart. How are c.n.s. and a.n.s. interconnected (a) structurally and (b) functionally?
- 5. What is a nerve impulse? How is an impulse transmitted through a nerve fiber? Across a synapse? What electrical phenomena take place during impulse transmission in a fiber?
- 6. What is the basic function of all sensory receptors? Describe the location and general structure of receptors for pain, touch, pressure, heat, and cold stimuli. Describe the location and structure of the taste and smell receptors. What are the primary taste sensations? Are tastes and smells inherent in given substances?
- 7. Describe the structure of the eye. What components form the focusing mechanism, and how is the function of focusing carried out? What is the distribution pattern of

rods and cones in the retina? Review the chemical changes leading to impulse production in rods. Describe the pattern of the neural pathways between the eyes and the brain.

8. Describe the structure of the ear. What components form the receptors for (a) static body balance and (b) dynamic body balance? How do these receptors function? Describe the internal structure of the cochlea and the organ of Corti. Show how different sounds produce corresponding sensations of hearing.

9. What are the general functions of neural centers? Review the structural organization of the brain. What is the specific function of each major part or region? What is meant by pathway facilitation?

10. What are conditioned reflexes? Show how such reflexes might be established by pathway facilitation. How do conditioned reflexes contribute to learning, habit formation, and behavior development?

SUGGESTED COLLATERAL READINGS

Beidler, L. M.: Our Taste Receptors, Sci. Monthly, vol. 75, 1952.

Evans, R. M.: Seeing Light and Color, Sci. American, vol. 181, 1949.

Haagen-Smit, A. J.: Smell and Taste, Sci. American, vol. 186, 1952.

Katz, B.: The Nerve Impulse, Sci. American, vol. 187, 1952.

Liddell, H. S.: Conditioning and the Emotions, Sci. American, vol. 190, 1954.

Sperry, R. W.: The Eye and the Brain, Sci. American, vol. 194, 1956.

Wald, G.: Eye and Camera, Sci. American, vol. 183, 1950.
Walter, W. G.: The Electrical Activity of the Brain, Sci.
American, vol. 190, 1954.

Part Five

SELF-PERPETUATION: REPRODUCTION

Of all protoplasmic functions, reproduction happens to be among the most noticeable to the casual human observer. Metabolism occurs largely on an invisible, molecular scale. Control functions result in steady state, that is, in unchanged, even conditions. Adaptation and evolution occur on a scale so vast that man does not perceive them directly or obviously. But reproduction does take place on a directly perceivable, obvious scale. Moreover, reproductive processes are universal and very dramatic: now

there is one, then there are two. Hence the selection of reproduction particularly as a certain criterion of life.

To be sure, the deep significance of reproduction does not lie in its dramatic nature but in its results. We recall that we assigned "living" properties to the first of the ancient nucleoproteins largely because they possessed reproductive properties. These properties have been handed down in an unbroken succession from the first genes to all present genes, and they still form the basis of all reproductive events today.

In this series of chapters, we first examine the **patterns of reproduction** as they occur on the various levels of the protoplasmic hierarchy. We then proceed with accounts of the actual **reproductive processes** characteristic of each of the major groups of organisms.

CHAPTER 19

The pattern of reproduction

If we define reproduction broadly as extension of protoplasm in space and in time, then its fundamental importance as a self-perpetuative device is readily apparent. For the formation of new protoplasmic units makes possible replacement and addition at every level of organization. Among molecules or cells, among organisms or species, replacement offsets death from normal wear and tear and death from accident or disease. Healing and regeneration are two aspects of replacement. Above and beyond this purely restorative function of reproduction,

addition of extra units at any level results in fourdimensional *growth*, that is, geographic, spatial expansion and extension in time.

Any new protoplasmic unit resembles the old, and reproduction therefore implies exact duplication. To create new units, raw materials are required. Indeed, reproduction at any level depends on ample nutrition specifically and on properly controlled metabolism generally. It is also clear that duplication of a large protoplasmic unit implies prior or simultaneous duplication of all con-

stituent smaller ones. Hence reproduction on the molecular level is the foundation for reproduction on every other level.

In this chapter we shall deal with the patterns of molecular, cellular, and organismic reproduction. And in the course of this, we shall also relate reproduction to development and to sex.

MOLECULAR AND CELLULAR REPRODUCTION

The patterns

The reproduction of molecules may take four different forms, according to the nature of the molecule to be reproduced. We are already familiar with all four (Fig. 19.1).

If water or another inorganic substance is to be reproduced within a cell, additional molecules of such substances must be supplied ready-made by nutrition. We note that accumulation is the simplest form of molecular "reproduction."

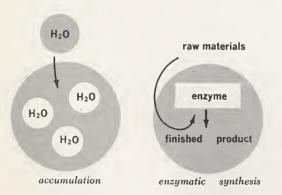
If a carbohydrate, a fat, or any of their numerous derivatives is to be duplicated, it may have to be synthesized from accumulated simpler raw materials with the aid of appropriate enzymes. So long as the enzymes of a cell remain the same, most newly synthesized organic molecules will automatically be exact duplicates of molecules synthesized earlier.

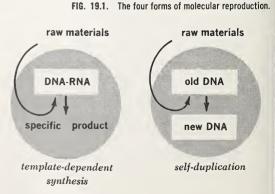
Thus the second form of molecular reproduction is enzymatic synthesis. It includes the first form, accumulation, as a component phase.

If a protein molecule is to be duplicated, we know that enzymes are required to link amino acids together. We also know that genes and RNA must provide specific blueprints, the templates for this linking. Hence the third form of molecular reproduction includes the first two, but is additionally characterized as template-dependent synthesis.

Lastly, if a gene is to be duplicated, it must serve as its own template and control its own replication (Chap. 16). All three other forms of molecular reproduction play a part here too. For phosphate must be accumulated; sugars, purines, and pyrimidines must be synthesized enzymatically; and protein must be synthesized with the aid of both enzymes and genetic templates. But in addition, duplication of genetic nucleoproteins hinges on specific self-duplication, and this is the fourth form of molecular reproduction.

In viruses, where the structural organization does not exceed the level of the molecular aggregate, molecular reproduction is equivalent to reproduction of the whole unit. In all truly living systems, accumulation, enzymatic and template-dependent synthesis, and self-duplication contribute either to





normal molecular replacement within cells or to molecular additions to cells. The result is *cell growth*.

Such increase in cell size in turn may be followed by increase in cell number, i.e., reproduction of a whole cell. This reproductive process is cell division, or fission. In the vast majority of cases, cells divide by binary fission; i.e., one "mother" cell becomes two roughly equally large "daughter" cells. After a period of growth, daughter cells may divide in their turn, and successive cell generations so may follow one another.

In cells which possess a distinctly formed nucleus and chromosomes, division consists of at least two separate processes: cleavage of the cytoplasm into two parts and duplication of the nucleus and its chromosomes. The chromosomal changes and all events associated with them together are known as mitosis. The type of cell division in which it occurs is therefore referred to as mitotic division. Note carefully that "mitosis" is not simply another word for "cell division," but is a particular series of nuclear and chromosomal events in a particular type of cell division.

In the Monera, distinct nuclei and chromosomes are not present. Here cell division includes gene duplication but not mitosis. Moreover, certain cells which do possess chromosomes on occasion divide without demonstrable mitotic changes. Any division in which mitotic events are not evident is referred to as *amitotic division*.

Mitotic division

The first demonstrable event of mitotic division, and probably of amitotic division as well, is a chemical event which occurs well before microscopically visible changes can be detected: the DNA content of the cell nucleus doubles, and the genes and chromosomes reproduce. A certain amount of time elapses before the visible phases of cell division begin. These visible phases consists of four successive, arbitrarily defined stages: prophase, metaphase, anaphase, and telophase. The first three stages are characterized predominantly by chromo-



FIG. 19.2. Early prophase in animal mitosis. The nuclear membrane is just dissolving, and chromosomes are already visible. To either side of the nuclear region is a darkly stained centriole area. These areas develop after a single centriole has divided and the two daughter centrioles have migrated to opposite sides of the nucleus. From each centriole area fine fibrils are beginning to radiate out; i. e., asters are beginning to form. (General Biological Supply House, Inc.)

somal changes, and the last stage is primarily the stage of cytoplasmic cleavage.

Prophase. One of the first happenings of prophase is the division of the *centriole*. It will be recalled that such a granule is found in the cells of Protista and Metazoa and that it is situated just outside the nucleus. As soon as the centriole has divided, the two resulting granules behave as if they repelled each other. Migrating away from each other, they eventually attain stations at opposite sides of the cell nucleus.

As the centrioles migrate, they become the anchor points of conspicuous fibrillar structures which form at this time. Portions of the fluid cytoplasm surrounding a centriole transform into a less fluid gel, and fine gelated strands appear which radiate away from the centriole like the spokes of a wheel. This set of gel fibrils is appropriately called an aster. Gel fibrils also arise *between* the two migrating centrioles, looping from one granule to the other in flat curves. These fibrils constitute a spindle. As the centrioles move farther and farther apart, spindle and aster fibrils lengthen and increase in number (Fig. 19.2).

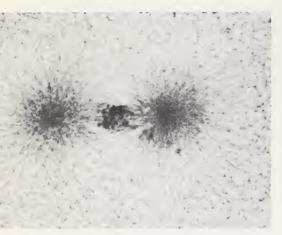
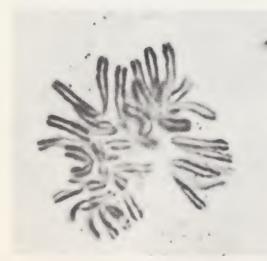


FIG. 19.3. Late prophase in animal mitosis. Asters are already conspicuous, and spindle fibers have formed between asters and chromosomes. The chromosomes are migrating into a metaphase plate. (General Biological Supply House, Inc.)

FIG. 19.4. At the time of prophase, chromosomes have already duplicated, and doubled chromosomes are therefore present. Each double is still held together at one point, the centromere. (General Biological Supply House, Inc.)



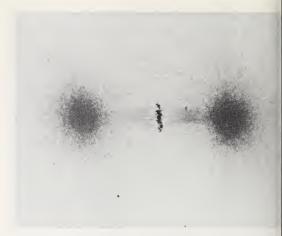


FIG. 19.5. Metaphase in animal mitosis. Note asters, spindle, and the metaphase plate, halfway along and at right angles to the spindle axis. Note also the fibrils which join the chromosomes lined up in the metaphase plate with the spindle poles. (General Biological Supply House, Inc.)

In Metaphyta, centrioles are not present and asters do not form. But a spindle develops nevertheless, and it again ranges from one end of the cell to the other. Spindles and, where present, asters and centrioles function as a sort of scaffolding for the principal events of mitosis (Fig. 19.3).

Preparations for these main events get under way even while the scaffolding is being erected. Still during prophase, the nuclear membrane dissolves away, the nucleoli present in the nucleus disintegrate, and nuclear and cytoplasmic substances mix freely.

Distinct chromosomes now become visible. Close examination reveals that each chromosome is a double filament (Fig. 19.4). As noted, each chromosome has manufactured a mathematically exact double some time before prophase. Such twin chromosomes lie closely parallel, and they are joined to each other only at a single point. This attachment point is called the centromere. Two spindle fibrils

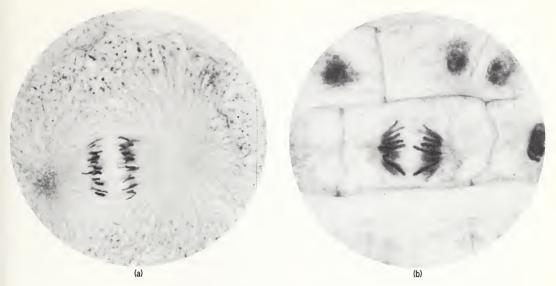


FIG. 19.6. Anaphase. (a) Mid-anaphase in animal mitosis. Chromosome sets are migrating toward spindle poles. (b) Anaphase in plant cell. Note absence of asters and centrioles but presence of spindle. (General Biological Supply House, Inc.)

become anchored to each centromere, one from each pole of the spindle. In this way, the chromosomes become linked to the fibril scaffolding. Prophase now is completed, and metaphase begins.

Metaphase and anaphase. Early during metaphase, the spindle poles, marked by centrioles in animal cells, reach their final position at opposite sides of the cell. Spindle and asters attain their maximal growth at this stage. The chromosome pairs, still scattered randomly through the central portion of the cell, now begin to migrate. If we draw an imaginary line from one spindle pole to the other, we mark out a spindle axis. Chromosomes migrate into a plane set at right angles to the spindle axis, midway along it. Specifically, it is the centromere of each chromosome pair which comes to occupy a station precisely within this plane. During the migration, the chromosomes trail behind their centromeres like streamers. Lined up in one

plane, the centromeres are said to form a metaphase plate (Fig. 19.5).

The lengthwise separation of the chromosome pairs now becomes complete. Each centromere divides, and so entirely independent chromosomes are produced. A small gel fibril arises at once between the centromeres of formerly joined chromosomes, and such chromosomes begin to move apart: once they are completely separated, the members of a pair of chromosomes behave as if they repelled each other. Thus one set of chromosomes migrates away from the metaphase plate toward one spindle pole, and an identical twin set migrates in the opposite direction toward the other spindle pole. The centromeres again lead, and the arms of the chromosomes trail. Also, the gel fibrils between twin centromeres lengthen, and fibrils between the centromeres and the spindle poles shorten. This period of poleward migration of chromosomes represents the anaphase of mitotic division (Fig. 19.6).

Telophase. The beginning of telophase is marked by the appearance of a cleavage furrow in animal cells and of a division plate in plant cells. Both furrow and plate form in the plane of the earlier metaphase plate. The cleavage furrow at first is a shallow groove circling the surface of a cell. This groove gradually deepens, cuts through the spindle fibrils, and eventually constricts the cell into two daughter cells.

Plant cells are divided into two by a partition of cellulose, the division plate, which is laid down more or less simultaneously at all points of the plane of cleavage.

While these events take place, the chromosomes within each prospective daughter cell aggregate near the spindle pole. Spindle fibrils and aster fibrils subside; that is, the protoplasm composing them reverts to a sol state. A new nuclear membrane now forms which envelops the chromosomes, but the centriole, if present, remains outside in the cytoplasm. Concurrently, the chromosomes in each newly forming nucleus manufacture new nucleoli, in numbers characteristic of the particular cell type. These nuclear processes terminate roughly when cytoplasmic cleavage nears completion, and mitotic division then has reached its endpoint (Fig. 19.7).

The net result of these occurrences is the cleavage of one cell into two cells containing precisely identical gene sets, incorporated in identical chromosome sets, and approximately equal quantities of all other protoplasmic constituents. Consequently, the structural and functional potential of both daughte cells is the same as that of the original mother cel

Mitotic potentials. In unicellular organisms, ced division is equivalent to reproduction of the wholo organism. In multicellular organisms, cell division either contributes to cell replacement, as in regeneration or wound healing, or adds to cell number. This leads to growth of tissues and organs (Fig. 19.8).

In this connection we may note that more highly specialized cells divide less frequently than less specialized cells. Adult nerve cells, for example, do not divide at all, but the less specialized cells of membranes divide often. We may note also that the most intense rates of cell division occur in embryonic stages, the least intense in old age.

What is the reason for this? With few exceptions, cellular reproductive capacity in the adult remains potentially as great as in the embryo. This is shown, for example, by the high rates of cell division in wound healing, in regeneration, in cancer, and in

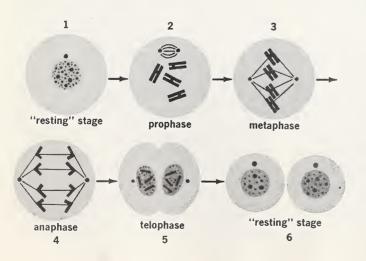


FIG. 19.7. Mitosis summary, diagrammatic. Note that a "resting" cell is resting only from the standpoint of reproductive activity. In all other respects it is exceedingly active.



FIG. 19.8. The overall pattern of reproduction.

tissue cultures. Such cultures are prepared by separating groups of cells from an organism and growing these in artificial nutrient solutions. Under such conditions, cells are found to reproduce faster than if they had remained within the natural organism.

Moreover, if newly formed cells in a culture are cut away from time to time, the original bit of tissue may live almost indefinitely long, certainly far longer than it would have lived within an organism. Through tissue culture, for example, a piece of the heart muscle of a chicken embryo has been maintained alive for over 30 years, which exceeds the usual life span of the whole chicken several times.

It is conceivable, therefore, that cell reproduction

in intact organisms may slow down mainly because the cells are *not* isolated, as in a tissue culture. Instead, cells are integrated very finely into a larger organization, where their reproductive potential is held in check. Occasionally, given cells escape this check, and normal healing processes or abnormal cancer may be the result.

ORGANISMIC REPRODUCTION

The patterns

After periods of tissue and organ growth by molecular and cellular reproduction, the whole multicellular organism may reproduce. The general pattern



FIG. 19.9. Vegetative reproduction in sea anemones. This animal is splitting lengthwise into two offspring organisms. (Courtesy of D. P. Wilson, Marine Biological Laboratory, Plymouth, England.)

consists of two phases. First, a portion of protoplasm, a reproductive unit, separates from the parent. Second, a duplicate organism then forms out of the reproductive unit, through development (Fig. 19.8).

In many cases, the reproductive unit consists of a substantial portion of the parent organism. For

example, certain flatworms, sea anemones, and other animal types may on occasion pull themselves apart into two or more portions. Each portion then regenerates the missing body parts (Fig. 19.9). In unicellular organisms, the whole body is the reproductive unit. Cell division in these forms is actually the only means of making more individuals. This general type of organismic multiplication, of particular importance in unicellular forms, is called vegetative reproduction. Its characteristics are that the reproductive unit is always a substantial part of the whole body and that such units are not specialized for reproduction primarily.

Closely allied to vegetative reproduction, and representing in fact a special form of it, is regenerative reproduction. Here the reproductive units arise fortuitously, as a result of injury to the parent by external agents. For example, many organisms may be cut into several pieces, and each piece may then grow into a new, whole individual. Almost any piece of a plant, a few segments of an earthworm, an arm of a starfish is an effective reproductive unit. The parent organisms which lose such sections of their bodies regenerate the missing parts (Fig. 19.10).

On theoretical grounds, a reproductive unit of a multicellular organism should not have to be a large portion of the parent organism. The smallest protoplasmic unit which possesses the genetic information and the operating equipment representative of an entire multicellular organism is a *single cell*. Hence the minimum unit for the construction of such an organism should be one cell. This is actually the universal case. Regardless of whether or not it may also reproduce vegetatively, every multicellular organism is capable of reproducing through single reproductive cells. All such cells are more or less specialized for reproduction, and they are formed in more or less specialized reproductive tissues or organs of the parent.

According to the manner of their formation and their later fate, two general classes of reproductive cells may be distinguished. One includes cells which may develop into adults directly. Such cells are very common in plants, where they are usually called

spores. Among animals, cells of this type are rarer, and they are given a variety of names. The designation bud cells is probably the most frequent.

Reproductive cells in the second general class cannot develop directly. Instead, they must first undergo a sexual process, in which two reproductive cells fuse. Such cells are called sex cells, or gametes. The gametes produced by a male parent are sperms; those produced by a female parent, eggs. Pairwise fusion of sperms and eggs is fertilization, and the fusion product is called a zygote. Development of gametes into adults cannot occur until fertilization has taken place.

We conclude that an organism may reproduce in one or more of three general ways (Fig. 19.11):

1. Vegetatively, by means of relatively large reproductive units, variously produced and not specialized primarily for reproduction

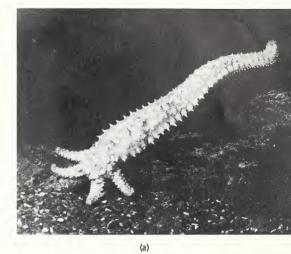
2. By means of spores or buds, specialized reproductive cells which develop directly of the latter

3. By means of gametes, specialized reproductive cells which develop only after a sexual process

As noted, vegetative reproduction is the basic process of multiplication in unicellular forms, but variants of it also occur widely elsewhere. Multicellular types reproduce mainly by the second and third methods. We may use the term sporulation to identify the second method and the term gametic reproduction to identify the third.

Note here that, in a strict sense, the often-used terms "asexual reproduction" and "sexual reproduction" are meaningless. In all forms of multiplication, the essential "reproductive" event is the formation of reproductive units. The rest is development. And it is this developmental phase which may or may not require sexual triggering. Reproduction as such, namely, the formation of reproductive units, is always "asexual."

Each of the three methods of reproduction has its own advantages and disadvantages. Where vegetative reproduction follows injury, the advantage is fairly obvious. And where vegetative reproduction occurs in whole unicellular organisms, the chief advantage is the possibility of very rapid increase



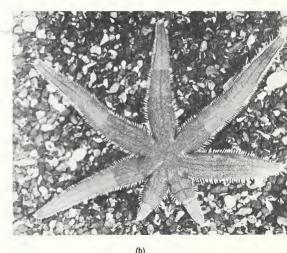
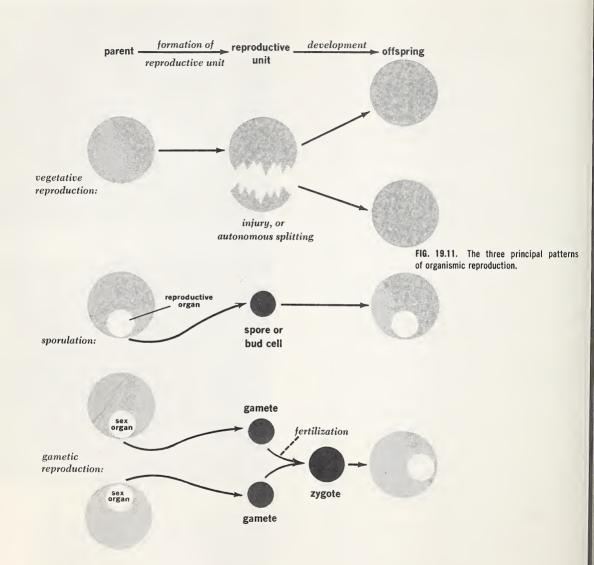


FIG. 19.10. Regenerative reproduction. (a) An arm of a starfish regenerates all missing parts and becomes a whole animal. (b) A starfish which has lost parts of each arm at least once regenerates into a whole animal. Note the lighter shading of the regenerated portions in each arm. The arm at top center has regenerated twice. (Courtesy of D. P. Wilson, Marine Biological Laboratory, Plymouth, England.)



in cell number. Sporulation too usually leads to rapid and abundant multiplication, and this method has an additional important advantage: spore cells can be produced either in water or in air. In water they can usually swim (e.g., by flagella), and in air they are protected by evaporation-resistant capsules and can be carried far by wind or animals. Thus spores are excellently adapted for wide distribution, and this is of major importance in organisms like plants, which cannot move themselves. One of the chief advantages of sporulation, therefore, is that it permits wide geographic dispersal.

Gametic reproduction entails serious disadvantages. For example, the method depends on chance, for sperms and eggs must meet and very often they simply do not. Meeting also requires locomotion, but eggs cannot move, nor can many organisms. Above all, gametic reproduction requires a water medium. In air, gametes would dry out quickly unless they possessed evaporation-resistant shells. But if two cells were so encased, they could then not fuse or exchange genes. However, gametic reproduction has one advantage which outweighs all the disadvantages so strongly that this method of reproduction has become practically universal. This advantage is not offered by the other methods of reproduction, and that is their major drawback. What only gametic reproduction can contribute is a result of the basic function of sex. We proceed to inquire into this function.

Sexuality

The process. The significance of sex is revealed most clearly in certain Protista where the sexual process is not even associated with reproduction.

For example, *Spirogyra* is a colonial green freshwater alga consisting of a long chain of cells, each of which is capable of living independently. Throughout spring, summer, and early fall, the cells reproduce vegetatively by cell division, adding to the length of the colony. Pieces of the filament may break off and settle elsewhere, starting new colonies. Later in the fall, two cells from two filaments lying

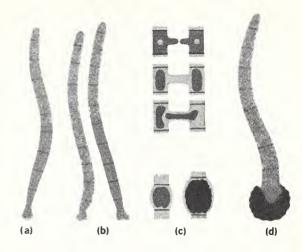


FIG. 19.12. Sexuality in Spirogyra. (a) Colony of cells. (b) Two filaments side by side prior to conjugation. (c) Protoplasmic bridge between opposite cells (top); migration of contents of one cell into the other (middle); formation of cyst, or zygospore (bottom). (d) Growth of new colony from opened zygospore. See also Fig. 19.14.

side by side may **conjugate:** a protoplasmic bridge forms which interconnects the two cells. The contents of one cell then pass through the bridge into the other cell, and the two protoplasms fuse (Fig. 19.12).

That is a sexual process. What initiates its occurrence, characteristically at that season of the year? Subsequent events provide the clue. All nonconjugated cells soon die as a result of falling autumn temperatures. But the fused double cell, the zygote, is able to secrete a heavy wall around itself. The cyst, or zygospore, so formed is then able to live through the winter. In the following spring, the cyst wall breaks open, and a new colony of cells then develops.

The protozoon *Paramecium* provides another instructive example. Here too reproduction occurs vegetatively through cell division and mating is

achieved through conjugation. However, the sexual process does not involve the permanent *fusion* of whole cells, but merely the *exchange* of gene sets (Fig. 19.13).

Note, first, that the sexual process is fundamentally quite distinct from reproduction. Spirogyra and Paramecium do not "multiply" by sex—if anything, quite the contrary. In Spirogyra, two cells form one, and in Paramecium, two cells enter the process, two cells again emerge. In all other organisms, sex and reproduction are just as equally distinct, even though the two processes may occur together.

Note further that in Spirogyra, in Paramecium, and in virtually all other organisms, man not excepted, sexual activity is particularly evident during periods of persistent stress. Sexuality may be brought out or intensified by unfavorable climates, by widespread food shortages, by overpopulation, by wartime activities, or by other similar stress conditions.

Indeed, most organisms in temperate climates manifest sexual activity typically in the fall or in the spring. Initial unfavorable changes in the fall environment bring forth sexual responses anticipating the worse conditions of winter, and sexual activity during spring anticipates the stress conditions of summer heat and dryness.

The function. Just how is sexuality effective against conditions of stress? Events in Spirogyra and Paramecium supply the general answer: every zygote resulting from the sexual process possesses

the genes of both cells which entered the process. Thus sex may be defined as the accumulation, within a single cell, of genes derived from two relatively unrelated cells.

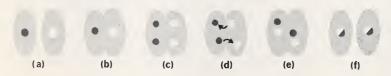
Sex therefore counteracts stress conditions on the principle of "Two are better than one." If the self-perpetuating powers of two relatively unrelated parent organisms are joined, through union of their genes, then the resulting offspring organism may acquire a survival potential which is greater than that of either parent alone. Because sex combines genes, and because such genetic change may be advantageous for survival, it is clear that sex has adaptive value.

That is the key point. Sex is a process of adaptation, not of reproduction.

Since every organism must adapt, sex has become universal. And since sex is a process involving single cells, it must be carried out at a stage when an organism consists of but a single cell. In unicellular organisms, therefore, sex may occur at any stage of the life cycle, regardless of when reproduction occurs, and it may be dissociated completely from reproduction. Indeed, the predominant life-cycle pattern among unicellular organisms is simply a succession of vegetative generations. Sex may occur at any point in such a succession, once or several times, under the influence of environmental stress.

By contrast, the life cycle of a multicellular organism usually passes through a unicellular stage only once, and if sex is to take place at all, it must take place then. Hence "gametic reproduction": sex occurs after the formation of reproductive cells and

FIG. 19.13. Sexuality in Paramecium. (a) Original partners. (b) Mating. (c) Nuclear division. (d) Gene exchange. (e) Result. (f) Nuclear fusion and separation of partners. Note that sexuality in Spirogyra involves fusion of two entire cells; in Paramecium, only exchanged nuclei fuse.



before the development of such single cells into multicellular organisms. Fertilization in such organisms has a dual function. It makes sex possible, i.e., it permits the pooling of the genes of sperm and egg. And second, it supplies the signal which triggers the start of development, thus ensuring that development does not begin before sex has occurred.

We may recognize now how each of the three basic reproductive methods plays its unique role in the propagation of organisms. In unicellular types, the main method is vegetative multiplication and sex occurs as a separate process at one or more points in the vegetative succession. In virtually all multicellular organisms, sex occurs as a phase of gametic reproduction. This method therefore is of combined propagative and adaptive value. If the adults can disperse geographically through locomotion, gametic reproduction usually is the main or only form of multiplication and sporulation does not occur. But if the adults are sessile, sporulation is an additional, species-dispersing method of reproduction. We shall see in following chapters how various organisms actually incorporate these reproductive processes into various life cycles.

Sex types. In Spirogyra, Paramecium, and indeed in most Protista, both sexes look exactly alike. There is no structural distinction between males and females, and the gametes are not visibly distinguishable as sperms and egg. Nevertheless, invisible chemical and functional differences do exist. Not any two gametes can conjugate. The cells of a Spirogyra filament, for example, have all originated from the same zygospore and may be regarded as being of the same "sex," or better, the same mating type. Cells within such a filament cannot unite sexually. Two cells from two different filaments are required (Fig. 19.14). Mating types exist in Paramecium as well, and cells from different ones are necessary for sexual union.

In other organisms, chemical sex differences are accompanied by visible, structural ones. True male and female sexes may be distinguished here. Specialized sex organs, ovaries and testes in animals,

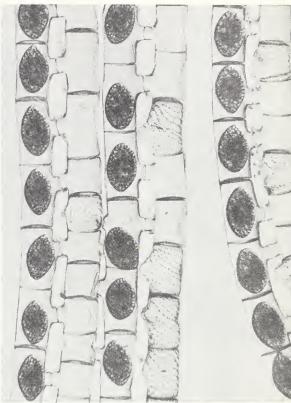


FIG. 19.14. Zygospore cysts of Spirogyra after conjugation. Note that all cells within a given filament have the same sexual properties: they may be either migrating sexual partners or stationary partners which receive the cells from a neighboring filament. All cells of a given filament are of the same mating type, and this accounts for the uniform sexual behavior. (General Biological Supply House, Inc.)

archegonia and antheridia in plants, produce eggs and sperms, respectively. Accessory structures may be present which, functioning in gamete transport and the later development of embryos, make up a reproductive system.

In most cases, a given individual is either a male or a female. But in very many species of organisms,

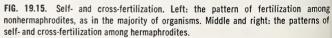
a given individual may possess both male and female reproductive systems within the same body. This condition is known as hermaphroditism. Most terrestrial plants are hermaphroditic, and among animals the phenomenon occurs in clams, for example, and also in earthworms, flatworms, and many other types of worms. Hermaphroditism sometimes develops as an abnormality in vertebrates, man included.

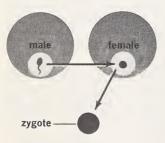
Hermaphroditism is a direct adaptation to the slow or sessile way of life. Since a normal hermaphrodite functions both as a male and as a female, it may not have to search for a mate at all: self-fertilization may take place. This is actually relatively rare, but it does occur in some animals and a number of plants. Most hermaphrodites, like all other organisms, must carry out cross-fertilization; that is, the sperms of one individual must fertilize the eggs of another individual (Fig. 19.15). The advantage of hermaphroditism here is that fewer reproductive cells are wasted. For example, if a given plant species is hermaphroditic, sperms from one individual may meet eggs in any other individual, for every hermaphrodite contains eggs. In sessile nonhermaphrodites, by contrast, many sperms would be wasted through chance misdistribution to the wrong sex. Similarly, if cross-fertilizing hermaphrodites are capable of some locomotion, like earthworms, for example, then fertilization becomes possible whenever *any* two individuals meet (Fig. 19.16). Since sluggish individuals are not likely to meet very frequently to begin with, and since every such meeting may result in fertilization, the adaptive value of hermaphroditism is clear.

Since fertilization always joins the nuclei of two cells, it is clear that sexuality has a doubling effect on chromosome (and gene) number. In the course of successive sexual generations, therefore, chromosome numbers would double progressively and indefinitely. But since chromosome numbers are known to remain constant, as species-specific traits, progressive chromosome doubling through sex evidently does not occur. What prevents it from occurring is the process of meiosis, universally correlated with sex.

Meiosis

In any life cycle which includes sex, meiosis takes place. If sex occurs once, meiosis occurs once too. The specific function of meiosis is to counteract the chromosome-doubling effect of fertilization. In different organisms, meiosis takes place at different points in the life cycle. In animals, meiosis occurs during the formation of gametes. For purposes of illustration, we shall here discuss this animal pattern.

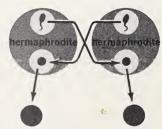




fertilization among separate sexes



hermaphroditic self-fertilization



hermaphroditic cross-fertilization



FIG. 19.16. Copulating earthworms. These animals are cross-fertilizing hermaphrodites. Hence whenever any two of them meet, each may be fertilized by the other. (General Biological Supply House, Inc.)

The pattern. We know that gametes are manufactured in the reproductive organs, i.e., the ovaries and testes. A first step in this manufacture consists in the production of new cells by mitotic division, just as in the formation of new cells in any other tissue. In a second step, the new cells then undergo a special process maturation, which transforms them into specialized reproductive cells with unique properties.

This maturation consists of cytoplasmic and nuclear phases. Cytoplasmic maturation includes, for example, growth of a tail-like flagellum in cells destined to be sperms, or accumulation of yolk in cells destined to be eggs. Nuclear maturation is meiosis. In this, the chromosome number of any cell destined to be a gamete is reduced by half. As a result, any mature sperm or egg possesses only half the original number of chromosomes. The unreduced number, before meiosis, is called the diploid number, and it is symbolized as 2n. The reduced number, after meiosis, is the haploid number, and it is symbolized as n.

Thus mature gametes are haploid, n. When two such gametes fuse in fertilization, the resulting zygote will be in a diploid, 2n, condition. This

zygote then develops into an adult consisting of cells all of which are still diploid. And when such an adult in turn produces gametes, the maturation of these gamete cells includes meiosis. Through this, the diploid 2n condition is reduced to a haploid n condition. Fertilization subsequently restores the 2n number again. In man, the diploid chromosome number of adult cells is 46. After meiosis, each mature human sperm or egg is haploid and contains but 23 chromosomes. During fertilization, the diploid number of 46 is reestablished. We note that the species-characteristic diploid number of 46 is maintained throughout successive sexual generations: meiosis always counteracts the doubling effect of fertilization (Fig. 19.17).

A diploid cell does not contain a 2n collection of mutually different chromosomes but a collection of n mutually different pairs of chromosomes. For a fertilized egg receives one haploid, n, set of chromosomes via the sperm and a like haploid set via the egg. Therefore, like shoes, the chromosomes of any diploid cell come in pairs. One of each pair originates initially in the sperm, the other in the egg. In an adult man, for example, 23 of the 46 chromosomes of every diploid cell are paternal, that is, they

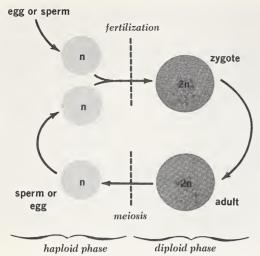


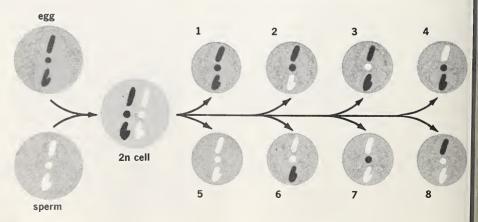
FIG. 19.17. The relation of meiosis to life cycle (animals). In man, n=23.

have been inherited originally from the father of that individual. The other 23 chromosomes are maternal, having been inherited from the mother. Each haploid set of 23 chromosomes represents one complete set of genes, and each diploid cell of the adult therefore possesses two complete sets of genes.

During gamete production in such an adult, chromosome reduction occurs in such a way that the mature haploid sperm or egg contains one of each maternal-paternal pair of chromosomes. In this haploid gamete, it is entirely a matter of chance which, and how many, chromosomes will be maternal and which and how many will be paternal. In a human sperm or egg, for example, 23 chromosomes make up a complete haploid set, and of these, a chance-determined number will be paternal, the remainder maternal. But the total of 23 will still represent one complete set of genes (Fig. 19.18).

The phrase "chromosome reduction" might imply that one of each pair of chromosomes is destroyed

FIG. 19.18. Each diploid cell contains two like sets of chromosomes, representing maternal-paternal pairs. The maternal set originated in the egg, and the paternal set in the sperm (left part of diagram). When later the chromosome number of a diploid cell is halved by meiosis, a resulting haploid cell contains a single set of chromosomes consisting of a chance-determined number of paternal and maternal chromosomes. The right part of the diagram shows the various possible paternal-maternal combinations if n=3.



or otherwise lost. This is not the case. Instead, chromosome number is reduced to half by two meiotic cell divisions. The general pattern of these divisions is as follows. An immature, diploid sex cell undergoes two successive cytoplasmic cleavages, which transform the one original cell into four cells. At the same time, the 2n chromosomes of the original cell duplicate once. As a result, 2n becomes 4n. And of these 4n chromosomes, one n is incorporated into each of the four cells formed. In sum, one original diploid cell becomes four mature haploid cells. In man, the 46 chromosomes of an immature sex cell double to 92 and the cytoplasm of that cell concurrently divides twice, producing four cells. These four share the 92 chromosomes equally. Each mature human gamete therefore contains 23 chromosomes (Fig. 19.19).

The process. The two meiotic divisions occur one after the other, and they have many features in common with mitotic divisions. For example, each meiotic division passes through prophase, metaphase, anaphase, and telophase, as in mitosis. As in mitotic divisions also, the centriole divides, spindle fibrils and asters form, and the nuclear membrane dissolves during each prophase and re-forms during each telophase.

The critical difference between mitosis and the *first* meiotic division lies in their metaphases.

In mitosis, we recall, the 2n chromosomes, each of them already duplicated, migrate into the metaphase plate, where all the centromeres line up in the same plane. Hence the mitotic metaphase plate is made up of 2n pairs of chromosomes.

In the first *meiotic* division, the 2n chromosomes similarly duplicate during or before prophase. These 2n pairs, the members of each pair again joined at the centromere, also migrate into the metaphase plate. But now only n pairs assemble in one plane. The other n pairs migrate into a plane of their own, a plane which is closely parallel to the first. Moreover, every pair in one plane comes to lie next to the corresponding type of chromosome pair in the other plane. Hence the metaphase

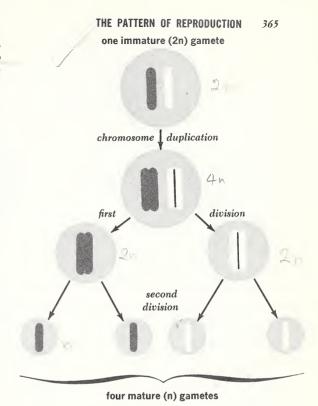


FIG. 19.19. The general pattern of events during meiosis, on the assumption that $2n=2. \label{eq:pattern}$

plate is made up of paired chromosome pairs, or foursomes of like chromosomes lying side by side. And there are n of these foursomes in the whole plate (Fig. 19.20).

During the ensuing anaphase, two chromosomes of each foursome migrate to one spindle pole, two to the other. At the end of the first meiotic division, therefore, there are two cells, each with n pairs of chromosomes. In the metaphase of the subsequent second meiotic division, the n pairs of chromosomes line up in the same plane, and n single chromosomes eventually migrate to each of the poles during anaphase. Hence, at the termination of meiosis

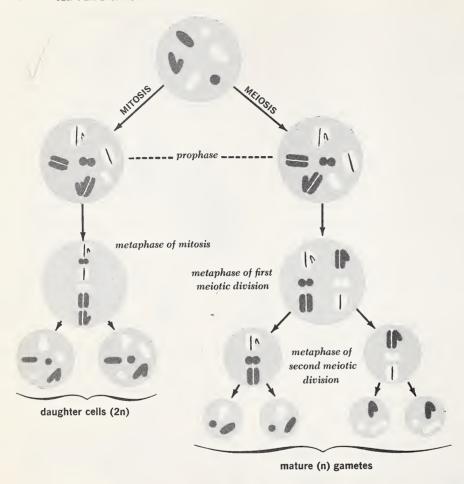


FIG. 19.20. A comparison of mitosis and meiosis, on the assumption that 2n=6. Note that the key difference between the two processes is the way the chromosomes line up in metaphase.

as a whole, four cells are present, each with n single chromosomes, a complete haploid set (Figs. 19.20 and 19.21).

In males, all four haploid cells produced by

meiosis become functional sperms. In females, by contrast, only one cell becomes a functional egg. Of the two cells here produced by the first meiotic division, one is small and it soon degenerates. Its





FIG. 19.21. In the nematode Ascaris, 2n = 4. Shown here are meiotic stages during egg maturation. (a) The first meiotic metaphase. Each of the two pairs of chromosomes has duplicated, and two foursomes are lined up in the metaphase plate. (b) The first telophase, when one large and one very small cell are formed, each with four chromosomes. The small cell will degenerate and form the first polar body (see also below). The remaining cell then undergoes the second meiotic division, the metaphase of which is shown in (c). Of the two pairs of chromosomes here present, two, or n, will go into each of the two cells yet to be formed. One of these will be the egg, the other will degenerate and form the second polar body. The first polar body may be seen as a dark spot at the top of the photo in (c). Note also the dark central spot in all three photos. This is the sperm nucleus. When meiosis of the egg is completed, sperm and egg nuclei will fuse and fertilization will be accomplished. (Carolina Biological Supply Co.)

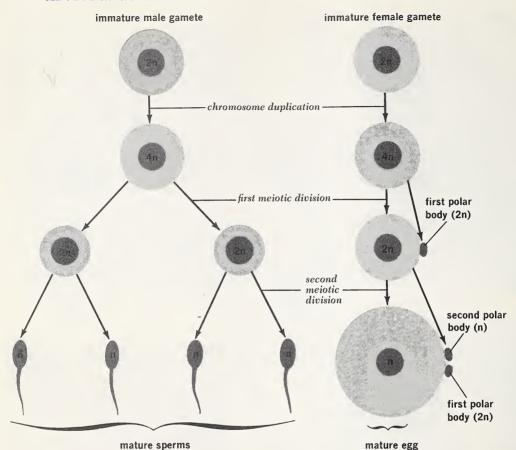


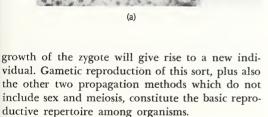
FIG. 19.22. Meiosis in males and females. In males, all four haploid cells formed become functional sperms. In females, one cell formed by the first meiotic division is small and degenerates and becomes the first polar body. Similarly, one cell formed by the second meiotic division becomes the second polar body. Thus only one cell matures as a functional egg.

remnants, now called the first polar body, remain attached to the other cell. This cell subsequently passes through the second meiotic division. Of the two cells produced now, one becomes the egg and the other again is small and degenerates. Its remnants form the second polar body, which, like the

first, remains attached to the egg (Figs. 19.21 to 19.23).

Having undergone meiosis and having concurrently matured cytoplasmically, ripe sperms and eggs now are ready to carry out their sexual function. And after fertilization, development and





In the following two chapters we inquire how this basic repertoire is actually executed in specific cases.



FIG. 19.23. Polar body formation. (a) A section through the edge of an immature egg of the whitefish, and the extremely eccentric position of the spindle and the chromosomes during a meiotic division. The chromosomes are in anaphase, and cleavage, which will occur at right angles to the spindle axis, will therefore produce an extremely large and an extremely small cell. (b) Cytoplasmic cleavage is under way. The small cell formed will degenerate, and the remnants will persist as a polar body. (General Biological Supply House, Inc.)

REVIEW QUESTIONS

- 1. How does reproduction contribute to steady-state maintenance? To self-perpetuation in general? Review the forms of molecular reproduction and the nature of each. How does molecular reproduction contribute to organismic reproduction?
- 2. What basic events occur in all forms of cell division? What is mitosis? Distinguish between mitotic and amitotic division. How does cell division contribute to organismic reproduction? Describe the process of mitotic division?
- 3. Distinguish between reproduction and development. What is vegetative reproduction? In which organisms, under what circumstances, and in which forms does vegetative reproduction occur?
- 4. What is sporulation? What is gametic reproduction? In which organisms does each of these occur? What is a spore? How is vegetative reproduction different from sporulation? How is sporulation different from gametic reproduction?
 - 5. What are the most basic events of every sexual

370

process? Under what conditions does sex tend to occur? In what way is sex of adaptive value?

6. Define mating, fertilization, zygote, gamete, mating type. What are the limitations of, and the environmental conditions required for (a) gametic reproduction and (b) sporulation? Contrast in detail.

7. What is hermaphroditism? In which organisms does it occur, generally and specifically? What is its adaptive function? Distinguish between self-fertilization and cross-fertilization.

8. What is the basic function of meiosis, and what makes such a process necessary? When, and where, does

meiosis occur, generally for all organisms and specifically for man? Define haploid, diploid.

9. How many pairs of chromosomes are found in a diploid cell? Of these, which and how many are maternal, and which and how many are paternal? How many chromosome duplications, and how many cell duplications, occur during meiosis? In what respects are mitosis and meiosis alike?

10. What is the essential difference between the metaphase of mitosis and the metaphase of the first meiotic division? Describe the complete sequence of events during both divisions of meiosis.

SUGGESTED COLLATERAL READINGS

- Biesele, J. J.: Tissue Culture and Cancer, Sci. American, vol. 195, 1956.
- Bishop, D. W.: Sperm Maturescence, Sci. Monthly, vol. 80, 1955.
- Braun, A. C.: Plant Cancer, Sci. American, vol. 186, 1952. Conklin, G.: Cancer and Environment, Sci. American, vol. 180, 1949.
- Farris, E. J.: Male Fertility, Sci. American, vol. 182, 1950. Gray, G. W.: Human Growth, Sci. American, vol. 189, 1953.
- Greene, H. S. N.: On the Development of Cancer, Sci. American, vol. 179, 1948.
- Mazia, D.: Cell Division, Sci. American, vol. 189, 1953.

- ——: The Life History of the Cell, Am. Scientist, vol. 44, 1956.
- Milne, L. J., and M. J. Milne: Animal Courtship, Sci. American, vol. 183, 1950.
- Stone, A.: The Control of Fertility, Sci. American, vol. 190, 1954.
- Tinbergen, N.: The Courtship of Animals, Sci. American, vol. 191, 1954.
- White, P. R.: Plant Tissue Cultures, Sci. American, vol. 182, 1950.
- Zahl, P. A.: The Evolution of Sex, Sci. American, vol. 180, 1949.

CHAPTER 20

Reproduction: Monera, Protista, Metaphyta

The three groups Monera, Protista, and Metaphyta share one reproductive characteristic in common: a given individual typically is capable of reproducing by all three basic methods. For example, in many Protista, a single individual may propagate either vegetatively, or through spores, or through gametes, or by two or even all three ways at different times. The "choice" of method is undoubtedly dictated by environmental conditions. Gametes are likely to be used under stress and food scarcity, spores under favorable situations and ample food supplies, and vegetative reproduction after injuries and also when conditions are favorable. In the Metaphyta, all three basic methods

occur too, but a "choice" no longer exists. These plants *must* reproduce by gametes as well as by spores, in a fixed life-cycle pattern; and vegetative reproduction largely has become a fortuitous process, which may or may not come into play, depending on injuries.

MONERA

Bacteria and blue-green algae reproduce vegetatively by cell division. Inasmuch as true chromosomes are not present, the fissions are a form of amitotic division (Fig. 20.1). Fissions may occur in exceedingly rapid succession, and the resulting huge



FIG. 20.1. The bacteria shown here are named Bacillus megatherium, and they are stained to show the cell walls. These organisms have grown in length for a period of time and, as the transverse partitions show, are now in various stages of reproduction by subdivision. (Courtesy of Dr. C. F. Robinow and the Society of American Bacteriologists.)

numbers of individuals are readily dispersed by wind, water, and other living organisms. Under stress, many bacterial types secrete heavy cyst walls around themselves, which protect the cells and keep them in a relatively inactive, dormant state, often for years. Such cysts are called "spores," or "resting spores." However, these are not specialized reproductive cells, and therefore they are not equivalent to the true spores of other organisms. Under favorable conditions, bacterial resting spores break open, and the emerging cells then resume their vegetative multiplication (Fig. 20.2).

Sex is completely unknown in the blue-green algae, the only phylum in the whole living world where this is the case. Till very recently, sex was also unknown in bacteria, but it is now definitely established to occur, in very rare instances under laboratory conditions. Whether or not it also takes place in nature is still not certain. Perhaps intensive investigation may uncover sex in blue-green algae as well.

In bacterial sexuality, pairs of cells *conjugate* and exchange genetic material. The mating partners then separate. A major reason why sex here has so long been unknown is that a mating pair is ex-

tremely tiny, not much different from two single, closely adjacent, unmated cells, and it is almost impossible to identify a mating pair among millions of closely packed cells. Indeed, mating was discovered first through its genetic results, not through direct observation. These genetic results have shown that bacteria are *haploid* organisms. Sex evidently introduces a diploid condition, and a reducing process, with effects like meiosis, must be presumed to take place. But since true chromosomes are not present, genetic reduction cannot be observed readily and its nature is still unknown.

If sex in Monera is at best rare, and mostly absent altogether, how do these organisms adapt to their changing environments? They may do so without sex, by their extremely rapid vegetative multiplication. Rapid reproduction means rapid evolution, through mutations. Hence even if millions of organisms succumb to one environment, a single survivor with appropriate mutations may, within a few hours, produce new millions of readapted organisms. Monera therefore rely on safety through numbers, and they, virtually alone among all living creatures, can do very well without sex.

PROTISTA

In this group, sexlessness is almost unknown (among the few exceptions are the familiar amebae, for example). Gametes, spores, and vegetative reproduction all occur. One feature of particular interest is that primitive Protista, notably the flagellate stocks among the algae and also some fungi, are haploid organisms. In these cases, haploid adults produce haploid spores or haploid gametes and fertilization gives rise to diploid zygotes. Then the very first event in a zygote is meiosis, which restores the typical haploid condition of the adult. Hence the life cycle is diploid only at the zygote stage. The alga Spirogyra provides a good illustration of such a life cycle (Fig. 20.3). As noted above, bacteria are rather similar in this respect.

This is probably very significant from an evolutionary standpoint. It suggests that the first Protista

and Monera, and perhaps even the first organisms of any kind, may have been haploid individuals. Such a primitive state may have been preserved in types like *Spirogyra*. In other words, in ancient, ancestral organisms, meiosis may have occurred immediately *after* fertilization, at the *start* of a new sexual generation. Indeed, it is reasonable that a primitive organism normally should possess only one complete set of genes, i.e., a haploid set, and that a chromosome-doubling process like fertilization should be *followed* by a chromosome-reducing process like meiosis. For fertilization is the stimulus to which meiosis is the response, and a stimulus ordinarily precedes a response.

But we know that in many Protista and in all animals, the adult formed after fertilization is diploid, not haploid. Such a condition could have arisen from the primitive pattern by a postponement of meiosis. For if meiosis did not occur immediately after fertilization, then a diploid adult would develop from a diploid zygote. In man, for example, meiosis is postponed as long as it can be postponed. It occurs at the time the diploid adult produces its own gametes, at the very end of a sexual generation. In other words, meiosis in man takes place just before fertilization, as if the response anticipated the stimulus (Fig. 20.4).

It is probable, therefore, that at various stages during the evolution of the Protista, shifts in the timing of meiosis may have occurred, which tended to make the adults diploid rather than haploid. One general advantage of such shifts undoubtedly is an increase in the genetic stability of the species. For if every chromosome in a cell is represented twice rather than just once, then every gene is represented twice too. This increases the redundancy of the genetic information (Chap. 16). Hence, even if one gene of a pair changes in some way, e.g., by mutation, the other gene would still preserve the original message. Another advantage of the diploid state will become apparent below.

We note, however, that many modern algae, many fungi, and probably all bacteria still feature the presumably primitive condition of haploid adults.

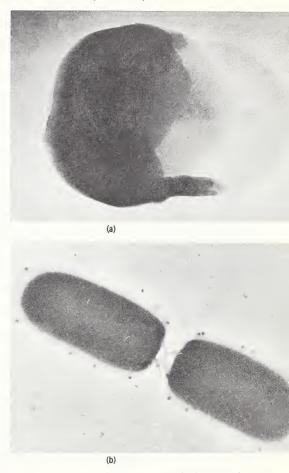


FIG. 20.2. (a) Electron micrograph of a germinating spore of the bacterium Bacillus mycoides. Note the bacterial cell emerging from the coat of the resting spore. (b) Electron micrograph of the bacterium Escherichia coli, at the end of vegetative reproduction by cell division. The daughter cells are almost completely separated. Note, incidentally, the small dark particles adhering to the bacterial cell walls. These are bacteriophage viruses, about to infect the bacterial cells. [Society of American Bacteriologists; (a) G. Knaysi, R. F. Baker, and J. Hillier, "J. Bacteriol.," Vol. 53, 1947; (b) S. E. Luria, M. Delbruck, and T. F. Anderson, "J. Bacteriol.," Vol. 46, 1953.1

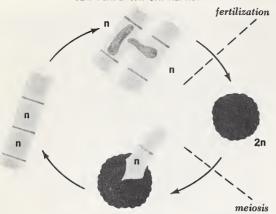


FIG. 20.3. Chromosome numbers in the life cycle of Spirogyra. Meiosis occurs after fertilization, and the cells of adult colonies are haploid.

Algae

Single-celled flagellate forms reproduce vegetatively by mitotic division. Sex usually occurs by fusion of two whole individuals which look alike, and the resulting zygote typically encysts. When the cyst wall later breaks open, meiosis is the first of events.

Reproductive processes in multicellular algae are extremely varied. In most species, swimming flagellate spores are produced. This is well illustrated in Ulothrix, a green filamentous type which superficially resembles Spirogyra. In given cells of Ulothrix, the cytoplasm may contract away from its cellulose housing and may divide a number of times within the housing. Each small cell so produced then matures into a flagellate spore. An opening subsequently forms in the cellulose wall, and the spores escape through it (Fig. 20.5a).

In somewhat similar fashion, this alga may also produce gametes. Given cells again divide within their cellulose walls, as in spore production. However, many more successive divisions occur, and many more, smaller cells are produced. These develop flagella, escape through an opening in the cellulose wall, and function as gametes; they must fuse pairwise (Fig. 20.5b).

The definition of the sexes is greater in algae such as Oedogonium, a green, filamentous plant structurally also rather like Spirogyra. In Oedogonium, a cell of one filament may enlarge and mature into a true, nonmotile egg. A cell of another filament

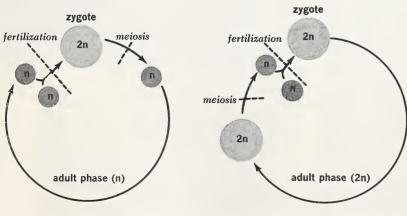
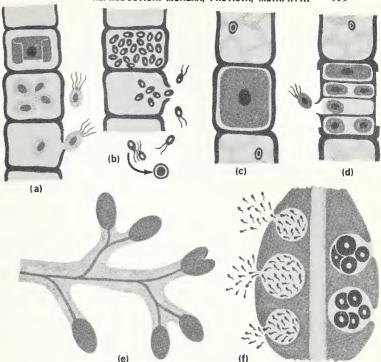


FIG. 20.4. The timing of meiosis in life cycles. In the primitive pattern, meiosis occurs just after chromosome doubling by fertilization. In the advanced pattern, meiosis is postponed to a point just before fertilization, which makes the adult diploid.

THE PRIMITIVE PATTERN

THE ADVANCED PATTERN

FIG. 20.5. Reproduction in a variety of algae. (a) Formation of flagellate spores in Ulothrix (top cell of diagram represents a nondividing cell). (b) Formation of flagellate gametes, and fertilization, in Ulothrix (note absence of sex differences among gametes). (c) A cell of Oedogonium developed into an egg. (d) A cell of Oedogonium divided up into a number of flagellate sperms. (e) A piece of the brown alga Fucus, with sexual reproductive structures at the tip. (f) Details of reproductive structures in Fucus; left half, sperm-producing organs; right half, egg-producing organs.



may subdivide into a number of true, flagellate sperms. If such swimming sperms happen to encounter egg-bearing filaments, fertilization may occur (Fig. 20.5c and d). In Oedogonium, as in Ulothrix, Spirogyra, and most filamentous algae, meiosis occurs just after fertilization; adults are haploid.

But as already noted earlier, in many algal groups the time of meiosis has shifted to a later point in the life cycle, and so adults are diploid. Such is the case, for example, in *Fucus*, a common brown alga found attached to rocks on the seashore. These plants exhibit a very high degree of sexual definition. Sperms and eggs are clearly different structurally, and these gametes are produced in distinct, rather elaborate male and female reproductive structures (Fig. 20.5e and f). Meiosis in algae like *Fucus* occurs before fertilization, not after, the tim-

ing pattern corresponding exactly to that of animals.

Most brown and red algae in general feature highly advanced reproductive cycles. These resemble the cycles encountered in the Metaphyta; that is, they consist of two alternating generations. One generation produces gametes and is sexual. The zygotes then develop into adults which produce spores. These grow into new adults, which are again sexual. Thus, unlike most of the other algae referred to above, brown and red types cannot "choose" between sporulation and gametic reproduction; they must carry out both methods in sequence.

Fungi

To illustrate reproductive processes in this group, we may examine events in the *bread molds* (Fig. 20.6). As their name indicates, these fungi subsist

376

FIG. 20.6. Reproduction in bread molds.

(a) Sporulation. Note the horizontal threads of mycelium, stalks with ripening spore cases, and escape of spores from the cases.

(b) Sexuality. Note the mycelial outgrowth on two neighboring hyphae, contact and fusion of sex cells, formation of encysted zygote, and development of zygote into stalk with spore case.

saprophytically on stale, decaying bread or on other starchy plant products. The body of the fungus is a dense meshwork of whitish protoplasmic filaments, the mycelium, which ramifies into the substance of bread. This mycelium may grow vegetatively by cell division. Also, the mycelial threads may develop many white stalks, which project outward from the bread and appear to the unaided eye as hairy fuzz. On the upper end of each of these stalks forms a tiny round chamber, the spore case, or sporangium. The tissues of this case produce many hundreds of cells, and these accumulate within the case and mature into encapsulated spores. The sporangium becomes black as the spores mature, and it eventually breaks open, allowing the ripe spores to escape. Wind or water then distributes the spores to other locations, and if the cells happen to fall on suitable raw material, they grow into new molds.

Gametic reproduction in bread molds occurs under conditions of stress. Two neighboring mycelial filaments may each develop a short side branch, one growing toward the other. The tip of each branch then matures as a sex cell. Sperm and egg cannot be distinguished, and we are evidently not dealing here with true sexes but with different mating types. The two gametes eventually make contact and fuse, and the resulting zygote secretes a heavy cyst wall around itself. Surviving adverse

conditions, the cyst may subsequently break open. The cell within then undergoes meiosis and may give rise to a new mycelium.

We may note that the adult body of bread molds is haploid, but this is by no means the case in all fungi. As among algae, shifts in the timing of meiosis have occurred also among fungi, and many fungi are diploid as adults.

In fungi generally, the functional details of sporulation and gametic reproduction are as above, even if structural details differ, often greatly. For example, the familiar stalked umbrella of mushrooms is a spore-producing structure. It is composed of many thousands of packed mycelial threads. On the underside of the umbrella are found gills, i.e., vertical plates arranged like the spokes of a wheel. These manufacture the spore cells. Mature spores break away and are dispersed passively (see also Chap. 7).

The most elaborate pattern of sporulative reproduction is encountered among the rusts, parasitic fungi which undergo complex life cycles involving several intermediate hosts. Within each such host, a different set of spores is produced. For example, the so-called wheat rust fungus manufactures, in succession, summer spores on wheat; winter spores on wheat; early spring spores on wheat stubble or in soil; spring spores on the leaves of barberry bushes,

after a sexual process has occurred, and then again summer spores on wheat. Each type of spore here develops into a fungal growth which produces the next spore type in the series.

Protozoa

Reproductive processes in protozoa, as in algae and fungi, are extremely varied in detail and often exceedingly complex. In very general terms, we may say that most protozoa are diploid organisms. Meiosis occurs just before fertilization, as in animals generally. However, one group within the phylum Sporozoa features haploid adult stages, and meiosis here occurs as in primitively algal flagellates, i.e., just after fertilization. Sex in protozoa may take the form of cell fusion, as in flagellate algae, or of conjugation and nuclear exchange (e.g., Paramecium and other ciliate protozoa; see Chap. 19). The basic method of reproduction is vegetative and is accomplished by mitotic fission. Encysted stages are quite common. However, these are not primarily reproductive in function but protective. Variants of true sporulation occur among the Sporozoa. In the Foraminifera (Phylum Sarcodina), life cycles with alternating sexual and asexual generations are known.

METAPHYTA

Since the Metaphyta trace back to green algal ancestors, the reproduction of the Metaphyta must trace back to such ancestors too. As we have just seen, these algal ancestors were aquatic, and they probably featured haploid adults, which could produce swimming gametes, swimming spores, or both. Meiosis presumably took place at the primitive time, i.e., immediately after fertilization, at the stage of the zygote. We have found also that some descendants of such ancestors probably shifted the time of meiosis to a very late point of the life cycle, i.e., to the time just before fertilization, at the stage of the gamete. Either of these stages was feasible, for both the zygote and the gamete stages are unicellular, and meiosis, like sex itself, must occur at a

unicellular stage of the life cycle. But there was also a third unicellular point in the life cycle, and it too could serve as the stage of meiosis. That third point was the stage of the *spore*. It became possible, therefore, to postpone meiosis from its primitive early timing to an intermediate point in the life cycle, when spores are produced (Fig. 20.7).

In such a case, the individual developing from a diploid zygote will remain diploid. At some time during its adult phase, that individual manufactures spores. Inasmuch as meiosis now occurs during spore manufacture, the spores will be haploid. Such spores develop into haploid individuals. These, during their adult phase, produce haploid gametes. Fertilization occurs subsequently, and a diploid zygote is formed. This completes the life cycle. It is this kind of cycle which has actually evolved in some Protista (e.g., brown and red algae). Above all, this is also the cycle which developed in the early Metaphyta and is still universal in all their modern descendants.

In effect, the shifting of meiosis to the time of spore manufacture produces a life cycle consisting of *two* generations of individuals: a diploid, spore-producing, asexual individual, representing what is called the sporophyte generation, and a haploid, gamete-producing sexual individual, representing the so-called gametophyte generation (Fig. 20.8).

In such an alternation of generations, the short diploid phase of the original ancestral life cycle is prolonged into a genetically stable, spore-producing adult and the original long haploid phase is correspondingly shortened. This is of immediate adaptive advantage to a terrestrial, sessile plant, and undoubtedly it is because of this advantage that such a cycle has become universal among Metaphyta. For to a sessile land organism, a waterrequiring sperm tends to be a distinct liability. Spores can be made evaporation-resistant, by encapsulation in shells, but sperms cannot, for they must swim and fuse with eggs. In other words, spores can be adapted to land life readily, but gametes not so readily. It is therefore highly advantageous if the terrestrial life cycle were to emphasize

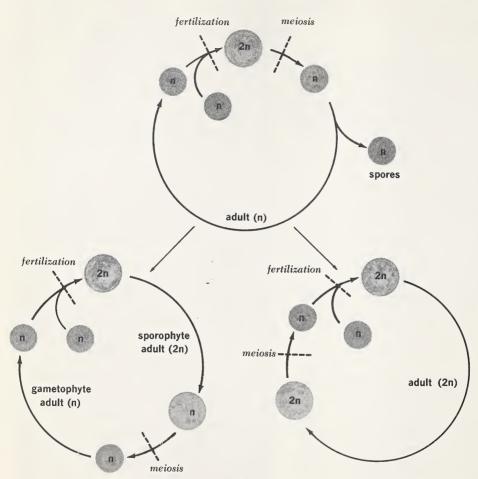


FIG. 20.7. The three points at which meiosis occurs in different life cycles. Top: the primitive timing of meiosis, just after fertilization. Lower left: the somewhat postponed timing, as in advanced spore-producing plants, leading to a two-generation life cycle with alternation of generations. Lower right: the most postponed timing, as in animals, leading to adult generations which are always diploid.

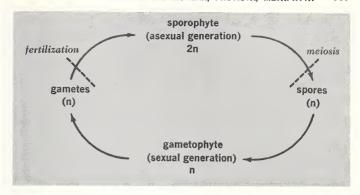


FIG. 20.8. The pattern of alternation of generations in plants.

the spore-producing phase and de-emphasize the water-requiring gamete-producing phase. This is precisely what an alternation of generations accomplishes.

As we shall see below, bryophytes have made a small step in the direction of emphasizing the sporophyte generation, and tracheophytes have gradually made a very large step.

Bryophyte reproduction

The problem of living and reproducing on land despite an aquatic inheritance has been solved by bryophytes in a number of ways. First, as just noted above, the two-phase cycle contains a land-adapted sporophyte generation which produces evaporationresistant spores. Second, the water-requiring gametophyte generation stays as close to water as possible; that is, the plants stay flat and small, hug the ground, and live in shady, more or less perpetually moist regions. Third, the time of sperm release and of fertilization is restricted to the time of the rainy seasons, when films of water covering the ground permit sperms to swim to eggs. And fourth, many bryophyte species develop as hermaphrodites, which ensures that sperms may meet eggs in any individual they happen to encounter.

The life cycle of mosses may serve to illustrate reproductive events in the phylum as a whole. As noted in Chap. 8, the main body of a moss consists of fine threadlike strands of green cells spread flat

over the ground. At certain seasons of the year, upright outgrowths develop on many points of the filamentous meshwork. These outgrowths, not higher than perhaps ½ or ½ in., are studded with tiny leaflike blades of tissue set on a central stalk (Fig. 20.9a). Dense clusters of such outgrowths form the familiar green "carpets" of mosses. These structures bear tiny sex organs at the stalk tips (Fig. 20.9b). In hermaphroditic species, both male and female organs develop on the same stalk. In other species, given stalks produce either male or female sex organs, but not both. Swimming sperms and sessile eggs are produced in these organs.

Fertilization can occur only if rain provides a water path for the sperms. In the hermaphroditic mosses, a single drop of water usually suffices to bridge the space between the male and female structures, set closely together on the same stalk. In nonhermaphroditic types, the stalked outgrowths are generally placed so densely that continuous water films may form easily from one stalk tip to another. Or raindrops may splash sperms to nearby stalks. If the second stalk happens to be of different sex, sperms bridging the gap may effect successful fertilization (Fig. 20.9c).

We note that fertilization in mosses, and in bryophytes generally, depends on the weather and on chance. Even a moderately dry climate prevents reproduction.

The parts of a moss discussed so far represent the

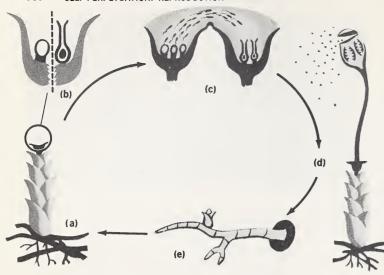


FIG. 20.9. The life cycle of a moss. (a) Moss shoot bearing sexual reproductive structures: (b) Detail of reproductive structures: left half, male sex organ; right half, female sex organ. (c) Fertilization; a drop of water forms a continuous pathway across two adjacent moss shoots. (d) A stalk with spore case develops from the fertilized egg. (e) A spore develops into a new moss filament.

gametophyte generation. The filamentous meshworks on the ground, the upright outgrowths, the sex organs, the gametes, all are haploid and constitute the sexual phase of the life cycle. The fertilized egg is diploid, however, and it represents the beginning of the asexual, diploid, sporophyte generation.

The zygote remains in the female sex organ and gives rise to many diploid cells. These grow as a thin straight stalk projecting upward for a distance of about 1/2 to 1 in. (Figs. 20.9d and 20.10). Although many cells in this stalk possess chlorophyll, the whole structure is nevertheless parasitic on the green part of the moss below. It not only withdraws needed water and inorganic materials, but depends also on extra carbohydrates, since its own photosynthetic capacity is apparently inadequate. At the end of each stalk develops a chamber, a spore case, in which spore cells are manufactured (Fig. 20.9d). During spore production, meiosis occurs. Ripened spores consequently are haploid, and this terminates the diploid phase of the moss life cycle. The spore case eventually breaks open, mature spores escape, and from them develop new, haploid, green moss filaments, the beginnings of a new sexual generation (Fig. 20.9e). The general pattern of the whole cycle is outlined in Fig. 20.11.

In bryophytes, the green gametophyte generation evidently represents the dominant, "main" part of the life cycle. The sporophyte generation is parasitic, is dependent on the gametophyte, and is produced only at certain times of the year. The gametophyte, with its water-requiring gamete, clearly is not as well adapted to land as the sporophyte with its encapsulated, "dry" spore. This is undoubtedly one of the reasons why bryophytes today enjoy only limited success.

Tracheophyte reproduction

A major distinguishing feature of the tracheophytes is that their sporophyte generation is the "main," dominant phase of the life cycle. The water-requiring gametophyte generation is highly reduced in size and life span, often extremely so. Thus, whereas the "familiar" plant in mosses is a gametophyte, the familiar plant in tracheophytes is a spore-producing organism. Because of this dominance of the sporophyte, tracheophytes are reproductively fairly independent of external water. This has con-



FIG. 20.10. Moss gametophytes bearing sporophytes on top. In the sporophytes, note stalks and terminal spore cases. (Carolina Biological Supply Co.)

tributed immeasurably to the success of these plants as terrestrial forms.

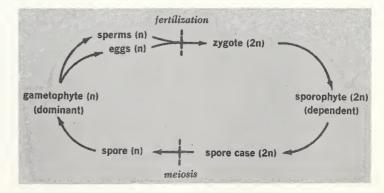
However, this success was won only gradually during evolution. Primitive tracheophytes today still reveal in their life cycle the difficulties which had to be overcome in a terrestrial existence. We shall first examine the reproduction of ferns, where the difficulties are still apparent, and then the reproduction of the more advanced seed plants, where the difficulties are largely solved.

Ferns. The plant customarily spoken of as a "fern" represents the diploid, asexual, sporophyte generation. It is large, leafy, green, and in direct contact with soil, and it persists the year round.

Spore-forming structures develop at certain seasons of the year on the undersides of fern leaves. Regular rows of brown spots, so-called sori, appear on the leaves. Microscopic examination demonstrates that each sorus is a shield of tissue raised from the undersurface of a leaf by a stalk (Fig. 20.12). Projecting sideways from this stalk and covered over by the brown shield are many smaller stalks, each bearing a hollow capsule at its tip. These capsules are spore cases, or *sporangia*. Many spores are manufactured in them, and during spore production, meiosis takes place; ripened fern spores are haploid. They represent the termination of the asexual generation and the beginning of the sexual generation.

Sporangia eventually rupture, and the escaping spores later develop into haploid gametophytes. Though everyone has seen ferns, i.e., sporophytes, few nonbiologists would be able to identify fern gametophytes. Each is a green plantlet consisting principally of a tiny heart-shaped plate of tissue, flat

FIG. 20.11. The overall pattern of reproduction in mosses.



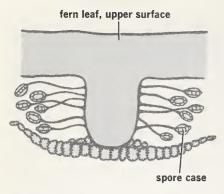


FIG. 20.12. A section through a fern leaf with a sorus on the underside. Stalks bearing spore cases project sideways, covered over by the brown shield of the sorus.

on the ground and measuring not more than about $\frac{1}{4}$ in. across (Fig. 20.13a). A number of cellular filaments projecting from the underside into the soil serve an absorptive function. This inconspicuous gametophyte, so unlike its large sporophytic partner, requires a moist, shady environment. In size, way of life, and function, the fern gametophyte is in fact wholly comparable with the moss gametophyte.

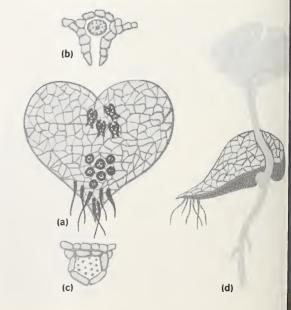
Sex organs develop on the gametophyte (Fig. 20.13b and c). As in mosses, the gametophytes of some fern species are hermaphroditic. Male sex organs are usually located near the tip of the heart-shaped plant, female sex organs near the notch. In other species, male and female organs are formed in separate individuals. The haploid sex organs manufacture haploid eggs and haploid, ciliated sperms. The pattern of fertilization is the same as in mosses; that is, rain is required to provide a water path for the sperms.

The diploid fertilized egg initiates a new sporophyte generation. Retained within the female sex organ, as in mosses, the zygote divides, and the resulting cells form a small sporophyte embryo. A tiny stem grows out from the female sex organ and curves into the soil, and a tiny embryonic leaf

similarly shoots up (Fig. 20.13d). At this stage, the embryo does not possess chlorophyll but depends on food supplied by the gametophyte, to which it is still attached. All this is clearly reminiscent of mosses. Soon the embryonic fern leaf matures and greens, and thereafter the embryo is on its own. Indeed, the gametophyte presently degenerates and dies off, leaving the young sporophyte as a separate, independent plant. The life-cycle pattern as a whole is outlined in Fig. 20.14.

We note that mosses and ferns do not differ too greatly in their gametophytes. Although ferns possess a highly developed sporophyte, well adapted to the realities of life on land, the gametophyte still poses a fundamental difficulty. For no matter how small and temporary the gametophyte may be, its water-requiring swimming sperms remain a weak

FIG. 20.13. (a) Diagram of fern gametophyte showing location of sex organs. (b) Female sex organ with egg. (c) Male sex organ with sperms. (d) Section through a gametophyte with young attached sporophyte.



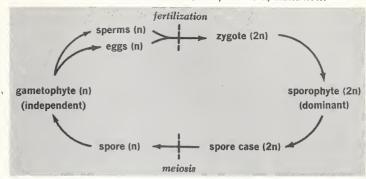
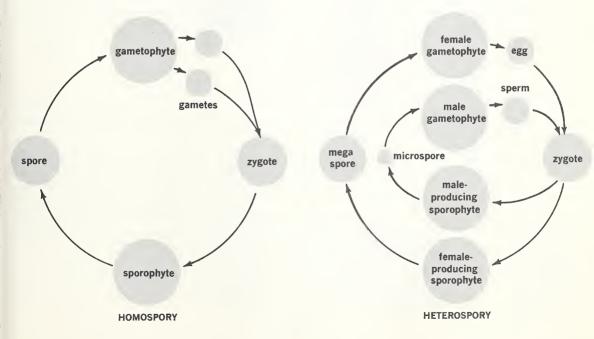


FIG. 20.14. The overall pattern of reproduction in ferns. Compare with Fig. 20.11.

FIG. 20.15. The homosporous and heterosporous life-cycle patterns of tracheophytes. In homospory, only the gamete stage is dual and sexually distinct. In heterospory, distinct male and female cycles exist which are merged only at fertilization.



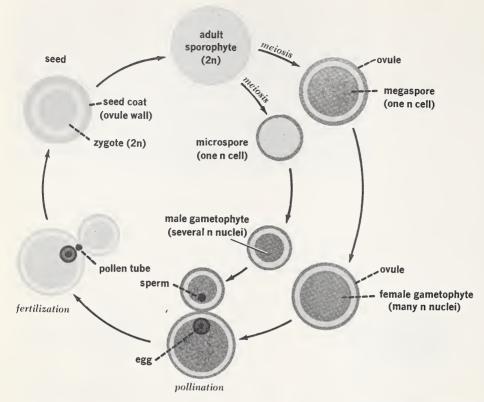


FIG. 20.16. The basic life-cycle pattern of seed plants.

link in a terrestrial life cycle. Primitive tracheophytes, ferns included, have never solved this dilemma. But the seed plants have.

Seed plants. We have just noted that in ferns, spores develop into gametophytes which carry either male or female or both types of sex organs. The plants here are said to be homosporous; that is, the spores are indistinguishable, and one cannot tell ahead of time whether a given spore will become a "male" gametophyte, a "female" gametophyte, or a hermaphrodite.

A different pattern is in evidence in all seed plants (and other primitive tracheophytes, some ferns included). Here the sporophytes manufacture two kinds of spores, one larger than the other. Larger megaspores consistently give rise to female gametophytes; smaller ones, called microspores, consistently give rise to male gametophytes (Fig. 20.15). Plants which produce two kinds of spores are said to be heterosporous. In seed plants, as we shall see presently, this heterosporous condition has aided in solving the problem of the water-requiring sperm.

The spore, well suited to dry land, produces the gametophyte, ill suited to dry land. Would it not resolve a good part of the difficulty if the gametophyte were made so small that it would never have to leave the sporophyte which gives rise to it? Could not the dominant sporophytes bear parasitic gametophytes, just as the reverse takes place in mosses? This has actually become the pattern in seed plants.

First, sporophytes manufacture two kinds of spores, as just noted above. This occurs in sporangia, or spore sacs. Many small male-producing microspores, familiarly known as pollen, are formed in spore sacs called microsporangia. Similarly, female-producing megaspores are developed in spore sacs called megasporangia, or ovules.

Second, within a spore sac, a given spore develops into a very small gametophyte consisting of just a few cells. Certain of these cells mature directly into gametes—sperms in male gametophytes, eggs in female gametophytes.

Third, instead of swimming sperms traveling through water to eggs, pollen grains containing male gametophytes and sperms travel through air, wind- or animal-borne, to ovules which contain female gametophytes and eggs. This process is called pollination, and it finally circumvents the need for external water.

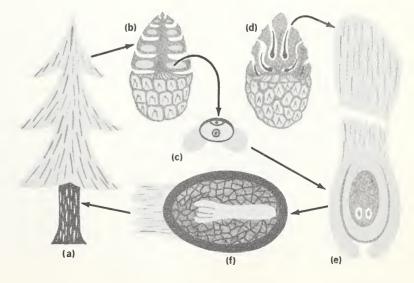
Fourth, after a pollen grain makes contact with an ovule, the sperm digests a path through the wall of the ovule to the female gametophyte within, and sperm and egg so may meet in a moist, protoplasmic environment.

Fifth, after fertilization is accomplished, the wall of the ovule hardens and, still retaining the zygote and the remnants of the female gametophyte within it, is then known as a seed. Such a seed later develops into a new sporophyte, and this completes the life cycle.

This basic pattern as a whole is outlined in Fig. 20.16. We now examine how it is executed specifically among coniferous plants and flowering plants.

Gymnosperms. A pine tree, for example, represents the dominant, diploid sporophyte. Its spore-producing structures are the pine cones. Two types of cones exist. A small variety, not longer than per-

FIG. 20.17. Diagrammatic representation of the life cycle of a pine. The adult sporophyte pine tree (a) produces either male cones (b) or female cones (d) or both. In the spore sacs of these cones are formed microspores or pollen grains (c) and megaspores (e). A megaspore develops into a small female gametophyte, which in turn produces eggs (e). Pollination occurs, and fertilization is brought about by means of a pollen tube (e). A seed then forms, in which the zygote develops into a sporophyte embryo (f).



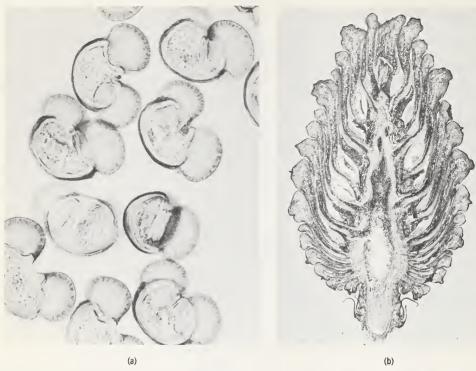


FIG. 20.18. Reproduction in the pine. (a) High-power view of pollen grains. Note the wing blades and the microspore cell in each grain. (b) Section through a megaspore-producing cone. Note the spore sacs between the cone leaves (actually on the upper surface of the leaves). [(a) Ward's Natural Science Establishment, Inc.; (b) General Biological Supply House, Inc.]

haps 1 in., has fairly tightly shingled cone leaves. Such cones produce microspores. The second type of cone is larger, roughly 3 in. long, and its cone leaves are rather widely spaced. Such cones produce megaspores. In many species of conifers, a given tree bears either one type of cone only or the other type only. Other species are hermaphroditic, both types being formed on the same tree.

In microspore-producing cones, the underside of each cone leaf carries two microsporangia. Numerous small pollen grains are manufactured in them (Figs. 20.17 and 20.18). During their maturation, meiosis occurs. A mature haploid microspore then usually divides twice, and the resulting four cells constitute the whole male haploid gametophyte. One of the four cells will later function as a sperm—nonciliated, for the first time in the history of land plants. As the cones ripen, they dry out and become brittle, cone leaves separate a bit, microsporangia rupture, and pollen grains, containing male gametophytes and sperms, escape. The pollen grains are equipped with a pair of tiny wing blades,

and as wind disperses them, some of them settle by chance in megaspore- or ovule-producing cones.

In the latter, the ovules are found on the upper sides of the cone leaves (Figs. 20.17 and 20.18). Each ovule is soft and green, and attached to it on one side is a long membranous wing blade. Within the ovule meiosis occurs, and one functional haploid megaspore is eventually formed. This spore divides many times, producing 2,000 or more cells. They represent the female gametophyte, and one of the cells later matures into an egg.

Pollen grains approaching such a cone may fall on the outer edge of a cone leaf. Since these leaves slant, pollen is likely to slide down into the angle formed by the cone leaf and the central cone stalk, to which the leaves are attached. At this angle lie the ovules with their mature female gametophytes. When pollen grains reach this region, pollination is accomplished.

Now the wall of the pollen grains ruptures. The male gametophyte within elongates into a pollen tube, which grows out through the rupture (Figs. 20.16 and 20.17). The functional sperm nucleus of the gametophyte lies in the advancing tip of the pollen tube. Before long, the tip of the tube makes contact with the soft wall of the ovule and digests a path through it. Once inside, the pollen tube grows toward the egg, and the sperm nucleus in the tip of the tube eventually fuses with the egg. This is fertilization. The diploid zygote so formed represents the beginning of a new sporophyte generation.

The remnants of the pollen grain and the pollen tube now degenerate, and the wall of the ovule hardens into a tough envelope. Within this envelope is found the tissues of the female gametophyte, plus a fertilized egg, which at once begins to develop into a little sporophyte embryo. The hardened ovule wall, together with its wing blade and its interior content, represents the *seed* (Figs. 20.16 and 20.17). Ripe seeds loosen from the cone leaves to which they had been attached, wind pressure bears on the wing blades, and seeds are dispersed. In favorable localities and under favorable climatic

conditions, seeds germinate, and new sporophyte pine trees develop from them.

We note that the gametophyte in gymnosperms is wholly dependent and parasitic and consists of but a few cells. The entire sexual, haploid phase of the life cycle has contracted in space into the pollen grain or the ovule and in time into a few short weeks at one season of the year, usually spring or fall.

Coniferous plants are the first to have completely shaken off the hampering inheritance of water-requiring sperms. This important evolutionary gain has been passed on unchanged to the later seed plants, the flowering plants. These have evolved various additional innovations, and through them they have become the most efficient land-reproducing plants of all.

Angiosperms. The diagram outlining the general life cycle of seed plants (Fig. 20.16) applies both to coniferous plants and to flowering plants. But the structures representing each phase are different in

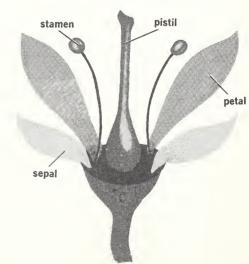


FIG. 20.19. Diagram of a simple flower.

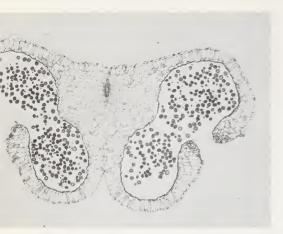


FIG. 20.20. Cross section through an anther of the lily. Note the two spore sacs, the openings in these sacs, and the microspores (pollen grains). (Ward's Natural Science Establishment, Inc.)

the two groups. In one group, the spore-producing organs are cones; in the other, they are flowers.

Some flowers are *composite*; that is, many individual flower units are carried collectively on a single plant as a large bloom (e.g., sunflower, dandelions, chrysanthemums, clover). Others are *simple* flowers; that is, each bloom here represents a single flower unit (e.g., tulips, lilies, buttercups). Not all flowering plants develop brightly colored blooms; consider, for example, the silks and tassels of corn. However, where colors and scents have evolved, they play an important role in pollination, by attracting pollen-dispersing animals.

A single flower unit typically consists, from the outside in, of a whorl of green sepal leaves, a whorl of usually pigmented petal leaves, a whorl of stamens, and a central pistil (Fig. 20.19).

A stamen is made up of a stalk carrying a composite spore sac, the anther, at its tip. In such a sac (Fig. 20.20) pollen grains are manufactured. Meiosis occurs during the maturation of a microspore. The ripe spore then develops into a cell with *three*

nuclei. This one cell with three nuclei represents the entire male gametophyte. Two of the three nuclei function as sperms. Clefts eventually form in an anther, through which pollen grains may escape.

Female reproductive parts are located in the pistil, in the center of a flower (Fig. 20.21). The upper part of the pistil, the stigma, is a sticky surface on which pollen grains will settle. A stalk, or style, connects the stigma with the bulbous lower part of the pistil, the ovary. This structure is a new evolutionary development, without equivalent in gymnosperms. In essence, the ovary is a thick-walled chamber which may be partitioned off into a number of sections. Each section holds an ovule. Within each ovule, one functional megaspore forms after meiosis, and this spore cell later comes to contain eight haploid nuclei. This eight-nucleate cell constitutes the entire female gametophyte. Typically, one of the eight nuclei and some surrounding cytoplasm mature as an egg (Figs. 20.21 and 20.22).

Most flowers are hermaphroditic and contain both stamens and pistil. In many groups of flowering plants, self-pollination is the rule. Pollen grains here simply fall on the stigma of the same flower. In other types, however, only cross-pollination leads to successful reproduction. In such flowers, many pollen grains undoubtedly do chance on the stigma of the same bloom. But such pollen grains may not begin to develop at all or may develop abnormally. Events proceed normally only when pollen grains from one flower are transferred to the stigmas of other flowers of the same species.

As might be expected, plants depending on wind for pollen dispersal manufacture huge numbers of pollen grains. Also, their flowers are relatively inconspicuous. By contrast, large, brightly colored, showy blooms form in plants which depend on animals for pollination. Such plants also manufacture abundant nectar, i.e., sugar water, as inducement. Many ingenious structural devices have evolved whereby only particular animal types have access to the nectar of a particular flower type. Potential "robbers" either cannot enter the flower or cannot

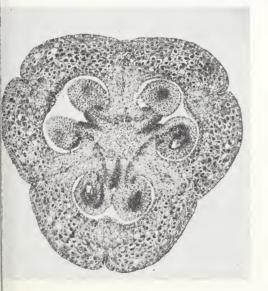
reach the nectar stores. On the other hand, "qualified" animals such as bees may find landing platforms, colored guide marks on petals, and other conveniences. And as these animals reach for nectar, deep down in the flower, they brush against stamens and pistil. In the process they pick up new pollen on their body surfaces or they deposit pollen from other flowers visited earlier. Aside from bees, animals which may carry out pollinating activity include certain wasps, butterflies, moths, in some cases small birds, and also men.

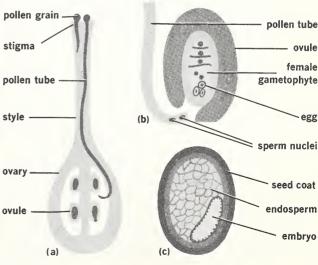
What happens after pollen grains have settled on a stigma, either through self- or through cross-pollination? One event is the rupturing of the wall of the pollen grain and the emergence of a pollen tube, as in pines. The two sperm nuclei are near the advancing tip of the tube. If several pollen grains have settled on a single stigma, several pollen tubes then grow. These digest a path through the stigma, through the style of the pistil, and into the

ovary (Fig. 20.21). If more than one pollen tube is present, only one eventually penetrates through to each female gametophyte in the ovary.

The tip of a pollen tube, carrying two sperm nuclei, thus reaches the female gametophyte. One of the sperm nuclei fuses with the egg, and the resulting zygote becomes the beginning of a new sporophyte embryo (Fig. 20.22). The second sperm nucleus contributes to another evolutionary innovation: it fuses with two female gametophyte nuclei. Since the sperm nucleus is haploid and since each of the female gametophyte nuclei is also haploid, the fusion product of one sperm and two female

FIG. 20.21. Diagram: (a) longitudinal section through a pistil; (b) the female gametophyte, with egg, and the advancing pollen tube carrying two sperm nuclei at the tip; (c) section through a seed. Photo: cross section through the ovary of a lily. Note the ovary wall (which will eventually give rise to the meat of a fruit) and the three pairs of ovules containing female gametophytes. (Photo, Ward's Natural Science Establishment, Inc.)





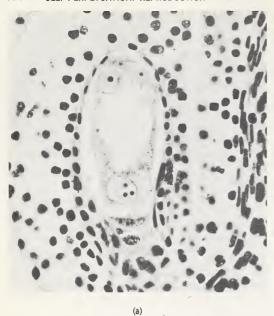


FIG. 20.22. (a) Section through a mature female gametophyte of the lily, surrounded by the tissue of the ovule. Eight nuclei are present in the gametophyte, the egg is mature, and fertilization may now occur. (b) Fertilization has taken place, and the zygote has developed into the young embryo shown here. (General Biological Supply House, Inc.)

(b) to enlarge and develops into a fruit. Many fruits are fleshy, like peaches. Here the expanded tissue of the ovary wall forms much or all of the "meat"

gametophyte nuclei is a triploid nucleus; that is, it possesses three sets of chromosomes. This triploid nucleus divides repeatedly and produces the socalled endosperm tissue. It soon fills all available space within the ovule and surrounds the sporophyte embryo more or less completely (Fig. 20.21). Endosperm tissue serves very largely as a reserve food store for the embryo. Until the young sporophyte has acquired a first green leaf, the endosperm provides it with nourishment.

While embryo and endosperm develop within the ovule, the wall of the ovule hardens and becomes the coat of a seed. At the same time, indeed as soon as fertilization has occurred, the ovary wall begins of a fruit. In other fruit types, e.g., nuts, the ovary wall develops into a dry, nonfleshy envelope surrounding the seeds.

We note that the reproductive pattern of flowering plants is characterized by three new features not encountered in coniferous plants: the flower itself, the inclusion of endosperm tissue within seeds, and the fruit, which contains a number of seeds. Each of these features is of pronounced adaptive value. The flower promotes pollination, the endosperm nourishes the embryo, and the fruit

promotes seed dispersal. For fleshy fruits may be eaten by animals, and seeds may be spit out or may be expelled undigested with the feces, in new locations. Dry fruits like nuts may be carried about by squirrels, for example, and may be left by them in some forgotten hiding place. Fruits with burrs, hooks, or wing blades are distributed widely by animals and wind. And fruits which simply fall to the ground eventually decay, which aids seed development by enriching a patch of soil.

Seed plants evidently have found a highly efficient solution to the problem of terrestrial reproduction, despite their sessile way of life and their consequent lack of access to permanent bodies of water. In these respects animals face fewer problems, but they too must solve the difficulty of the water-requiring sperms. They do so in their own way, as the next chapter will show.

REVIEW QUESTIONS

- 1. Review the basic life-cycle patterns of bacteria, algae, and fungi, with attention to differences between unicellular and multicellular forms.
- 2. Describe the processes of sporulation and gametic reproduction in (a) bread molds and (b) Ulothrix. Describe the process of gametic reproduction in (a) Spirogyra, (b) Oedogonium, and (c) Fucus. How does the degree of sexual definition differ in these three algal types?
- 3. At what points in the life cycles of different plants does meiosis occur? Which of these timing patterns is probably primitive, and in which plants is it encountered? Describe the life-cycle patterns of such plants, with attention to n and 2n phases.
- 4. How many other timing patterns of meiosis have evolved from the primitive pattern, and in which plants are they encountered? Describe these patterns. What is the timing pattern of meiosis in animals?
- 5. Describe the basic life cycle involving alternation of generations. How may such a cycle have evolved?

- What are its adaptive advantages? How has availability or nonavailability of water affected the reproductive evolution of plants?
- 6. Describe the detailed life cycle of a bryophyte. In what respects is it poorly suited to terrestrial life?
- 7. Describe the detailed life cycle of a fern. Compare with the life cycle of bryophytes; what is similar and what is different? What are the adaptive advantages of a prolonged 2n phase?
- 8. Distinguish between homospory and heterospory. In which plant groups is the latter encountered? Describe the basic life cycle of seed plants. In what ways is this pattern particularly advantageous for terrestrial life? Distinguish carefully between pollination and fertilization.
- **9.** Describe the detailed life cycle of coniferous plants. Define seed, pollen tube, self- and cross-pollination.
- 10. Describe the structure and adaptive significance of a flower. Define ovary, endosperm, fruit. Describe the detailed life cycle of flowering plants.

SUGGESTED COLLATERAL READINGS

Delbruck, M., and M. Delbruck: Bacterial Viruses and Sex, Sci. American, vol. 179, 1948.

Grant, V.: The Fertilization of Flowers, Sci. American, vol. 184, 1951.

Wollman, E. L., and F. Jacob: Sexuality in Bacteria, Sci. American, vol. 195, 1956.

CHAPTER 21

Reproduction: Metazoa

Animal meiosis typically occurs at the time of gamete manufacture. Hence animals are diploid, and the only haploid phase is the stage of the mature gametes.

A universal reproductive feature among animals is the occurrence of gametic reproduction. In *moving* animals, this form of multiplication tends to be the *only* method and species dispersal is accomplished by adult locomotion. Moving animals either live in water or can move to water; hence the water problem in sperm release never arises as it does in plants.

Sessile animals are all aquatic, and they too there-

fore never lack a water medium for their sperms. But such animals do have problems of species dispersal, and in these cases some form of sporulation commonly occurs in addition to reproduction by gametes. Sporulation generally involves the manufacture of *buds*, either single cells or small groups of cells (e.g., sponges, *Hydra*, Fig. 21.1). Buds grow, and then they usually separate from the parent. They swim about for some time, eventually settle, and develop directly into new adults. Being produced by diploid parents, the buds are diploid too. Buds and gametes usually can be produced by the same generation of individuals. But in the Hy-

drozoa (a class of the coelenterates) and also in the flukes (a class of flatworms), the life cycle consists of an alternation of generations somewhat reminiscent of plants; that is, a sexual, gamete-producing generation gives rise to an asexual, bud-producing generation, and vice versa (Chap. 9). However, both generations here are diploid.

Vegetative reproduction occurs in some animal groups, usually in the form of regenerative reproduction after injury (Fig. 21.2). In most animals, regeneration capacity is severely restricted and pieces separated from the parent simply die. In such cases the only remnant of vegetative reproduction is wound healing.

In this chapter we shall be concerned largely with gametic reproduction.

REPRODUCTIVE PATTERNS

Animal sperms are adapted for swimming and require water. If the adults live in water or can deposit gametes into water (e.g., frogs), then fertilization is accomplished quite readily. The parents spawn, i.e., shed their gametes, in permanent bodies of water, and sperms swim to eggs. This is called external fertilization. The zygotes develop into new individuals within that body of water.

Most land animals circumvent the need for external water through locomotion. For example, in earthworms, insects, spiders, reptiles, birds, and mammals, prospective parents move together and the male ejects swimming sperms directly into the body of the female, where protoplasm provides a water medium for the sperms. The gametes then meet within the body of the female, and this is internal fertilization.

Where fertilization is internal, fertilized eggs are handled in a variety of ways. They may be released by the female into natural bodies of water, where they develop (e.g., mosquitoes and many other insects). Or second, they may be released on land, after having been protected against evaporation by shells secreted around them (e.g., the egg cocoons of earthworms, spiders, and some insects and the



FIG. 21.1. Asexual development. Two buds are developing on this parental hydra, and when the buds are fully grown they separate from the parent and take up independent existence. (Courtesy of Dr. R. Vishniac, Albert Einstein College of Medicine, Yeshiva University.)

shelled land eggs of other insects, reptiles, and birds). The zygotes develop within such shells, and the young later hatch out. Or third, the fertilized eggs may be retained right within the female. There the developing young receive protection (as in some fishes, amphibia, and reptiles) or protection as well as nourishment (as in most mammals). In either case, the young are born as fully formed animals.

Regardless of the above patterns, an animal zygote typically matures in three developmental steps (Fig. 21.3). The first step is the growth and transformation of the zygote into an immature, still developing organism, the embryo. The embryonic phase then generally terminates through hatching, in which the embryo emerges from its original egg envelopes and becomes a free-living larva. This second phase of development is characteristic of virtually all animal phyla, but in certain subgroups within phyla, larval phases may be

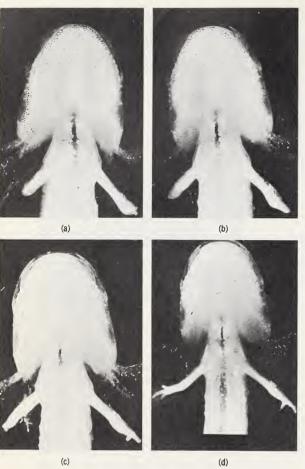


FIG. 21.2. Both arms of this salamander larva were amputated, one above and one below the elbow. (a) to (d) The degree of regeneration attained after 1, 14, 22, and 31 days, respectively. (Courtesy of Dr. C. Thornton, Kenyon College.)

absent (e.g., birds, mammals; see also below). Larvae are transient organisms playing a variety of roles. For example, they may function in geographic dispersal, especially if the adult is sessile or sluggish (e.g., clams, many worms, tunicates). Or they may

serve as temporary "feeding machines." They accumulate enough raw materials in the form of larval protoplasm to make lengthy further development possible (e.g., insect caterpillars). The larval period generally terminates with metamorphosis, a more or less sudden transformation into the third and last developmental phase, i.e., the adult.

In what follows we shall discuss this sequence of developmental steps in greater detail. We begin by considering reproductive systems and processes of gamete formation.

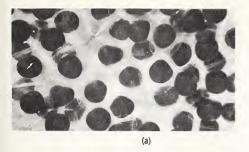
THE GAMETES

Reproductive systems

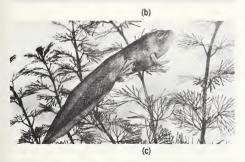
The basic structural plan of all animal reproductive systems is comparatively simple. The main components are a pair of gamete-producing organs, the testes in males, the ovaries in females. These organs are collectively known as gonads. They are each joined to a system of ducts, which carry the reproductive products, and usually also several glandular fluid secretions, to the outside of the body. In males, the ducts are sperm ducts; in females, they are egg ducts, or oviducts (Figs. 21.4 and 21.5).

Where fertilization is internal, the sperms swim up the oviducts and meet and fertilize eggs somewhere along the course of these ducts. Zygotes then are propelled down by cilia on the inner surface of the oviducts. Where the young develop within the body of the female, the lower section of the oviduct is enlarged into a chamber, the womb, or uterus. Fertilized eggs are propelled into it, and the young mature there.

In most animals, gametes are manufactured only at one period of the year, during a breeding season. However, some mammals, for example, apes and man, produce gametes the year round. In human males, sperm production begins at puberty, i.e., the time of sexual maturity, and may continue for life. In human females, egg production starts at puberty also and continues at a rate of roughly one per month for a period of about 30 years.









sperm duct
seminal vesicle
prostate gland
urethra
epididymis
testis
testicular tubules

FIG. 21.4. The male reproductive system, diagrammatic. Testis on left shown in section.

In vertebrates generally, gamete production is under the control of hormones. In human males, for example, the proper functioning of the reproductive system depends on the male sex hormone testosterone, secreted by the testes. But the testes in turn require a hormone stimulus from the pituitary gland. This gland secretes a "testis-stimulating hormone" (TSH), and under its influence the testes secrete testosterone. The latter then keeps the reproductive system operating, and so it indirectly also promotes sperm manufacture. Testosterone also has a feedback effect on the pituitary, inhibiting that gland from secreting too much TSH (Fig. 21.6).

FIG. 21.3. These stages in the life cycle of frogs symbolize the main stages in the sexual development of animals generally. Eggs, embryo, larva, and adult are shown. (Eggs, Carolina Biological Supply Co.; tadpole, American Museum of Natural History; others, General Biological Supply House, Inc.)

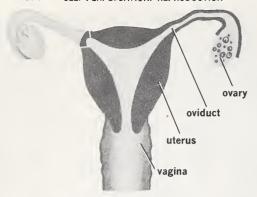
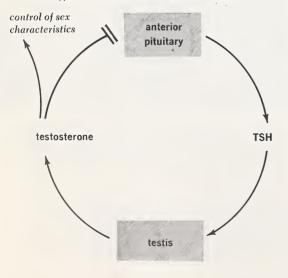


FIG. 21.5. Diagram of the female reproductive system.

Similar hormonal controls exist in human females. Indeed here, as also in apes and Old World monkeys, *two* hormonal feedback systems are integrated into rhythmic egg-producing cycles. These are called menstrual cycles.

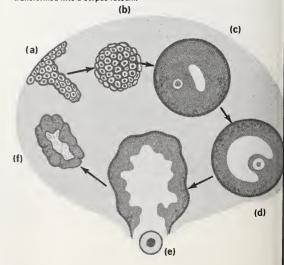
FIG. 21.6. The control of testosterone secretion. TSH is the "testis-stimulating hormone" secreted by the pituitary. Arrow tipped with transverse double bar denotes inhibition.



Menstrual cycles

In man, a menstrual cycle lasts about one month. In the ovaries, a maturing egg (undergoing meiosis at that time) is surrounded by other cells, so-called follicle cells. These plus the egg represent a follicle (Figs. 21.7 and 21.8). Growth of such a follicle occurs under the influence of a "follicle-stimulating hormone" (FSH) secreted by the pituitary gland. Under this stimulus, the follicle cells manufacture the female sex hormone estrogen. Like testosterone in males, estrogen keeps the female reproductive system in operation. It also has an inhibitory feedback effect on the pituitary, such that the FSH output of that gland is sharply reduced when high estrogen concentrations reach it via the blood (Fig. 21.9). This occurs after the follicle has grown for about 12 days. The egg is mature at that time, just when the follicle cells produce so much estrogen that the hormone inhibits FSH secretion by the pituitary. This reduction of FSH brings about a

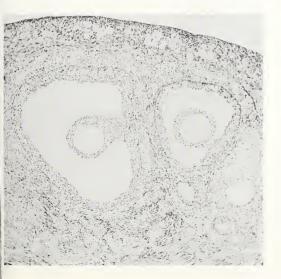
FIG. 21.7. The growth of an egg (diagrammatic). (a) and (b) Newly formed potential egg cells within the ovary. (c) and (d) Maturation of one of the cells into an egg and development of surrounding cells into a follicle. Note the enlarging follicular cavity. (e) Ovulation. (f) The remnants of the follicle have transformed into a corpus luteum.



rupturing of the follicle and the ovary wall, and the egg so escapes. It falls into the oviduct and is now ready to be fertilized. The process of egg escape is called **ovulation** (Fig. 21.7).

The old follicle cells remaining in the ovary now are no longer stimulated by FSH; hence they no longer produce estrogen. Instead, they transform into a yellowish body, the corpus luteum. This transformation is under the control of a new hormone secreted by the pituitary gland at this stage. The hormone is known as LH, short for "luteum-producing hormone." Under the influence of LH, the corpus luteum comes to secrete a new hormone of its own, namely, progesterone. This may be called the "pregnancy hormone," for it prepares the uterus to receive a fertilized egg. Progesterone

Fig. 21.8. Section through a mammalian ovary. Note the two large follicles, the follicular cavities, and the large egg cell in each follicle embedded within a mass of cells along the follicular wall. Near the top of the photo, along the edge of the ovary, note the relatively large cells. These are immature eggs which will become mature later, within follicles yet to be formed. (Ward's Natural Science Establishment. Inc.)



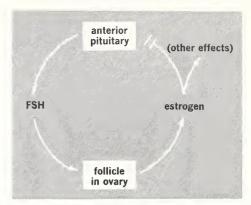


FIG. 21.9. The control of estrogen secretion. FSH is the "follicle-stimulating hormone." The arrow tipped with a transverse double bar denotes inhibition. Inhibitory concentrations of estrogen are reached after some 10 to 12 days of follicle growth.

stimulates the development of many new blood vessels in the uterus, in anticipation of the time when the fertilized egg and later embryo will require nutrients from the maternal blood.

If fertilization actually occurs, the corpus luteum continues to grow and more and more progesterone is secreted by it, and the zygote soon reaches the uterus and then develops there. But if fertilization does not occur, the increasing amounts of progesterone eventually have an inhibitory feedback effect on the pituitary, and that gland is then prevented from secreting more LH. This in turn stops progesterone production in the corpus luteum (Fig. 21.10). But without enough progesterone, the "ready" uterus cannot remain ready; that is, the newly formed blood vessels in its wall rupture and disintegrate, and blood escapes to the outside of the body. This is menstruation. The time between ovulation and menstruation is roughly 14 to 16 days. Thereafter, the pituitary resumes its manufacture of FSH, and a new month-long menstrual cycle begins. The sequence of events in a whole cycle is summarized in Fig. 21.11.

Menstrual cycles are essentially ways of producing eggs in a controlled, rhythmically timed manner. With or without such cycles, the production of gametes is the preliminary for fertilization and for subsequent development.

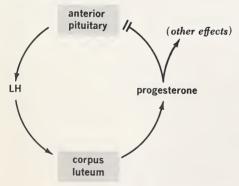
THE EMBRYO

Development

The pattern. In multicellular organisms generally, development brings about a transformation of a single cell, e.g., a zygote or a spore, into a whole adult organism. This is accomplished by two broad groups of processes, called morphogenesis and differentiation.

One component of morphogenesis is increase in size, or growth. This may occur by increase in the *number* of protoplasmic parts, by increase in the *size* of parts, by increase in the *spacing* of parts, or by two or all three of these in combination. In the

FIG. 21.10. The control of progesterone secretion. LH is the "luteum-producing hormone." The pituitary secretes LH under the stimulus of estrogen. The arrow tipped with a transverse double bar denotes inhibition. Inhibitory concentrations of progesterone are reached after some two weeks of corpus luteum activity. After progesterone inhibits the pituitary, that gland resumes FSH secretion. This starts a new menstrual cycle.



development of multicellular organisms, the most significant form of growth usually is increase in the *number of cells*, brought about by mitotic divisions. Thus large organisms differ from small ones mostly in cell number, not cell size.

A second component of morphogenesis is establishment of distinct organismic form. Clearly, protoplasmic parts like cells do not simply accumulate in random heaps, but they become organized into precise groupings and architectures, specific for given species. One form-producing process is differential growth. Here the amounts and rates of growth are unequal in different body parts, or they differ for different directions of space. This leads to localized enlargements, diminutions, elongations, thickenings, altered contours, layers, hollows, solid masses, or other expressions of form.

In addition to differential growth, the form of living matter is shaped and molded by form-regulating movements. This involves actual shifts and migrations of growing parts relative to one another. Through such movements, parts may pile up in one region and become thinned out in others. Compact masses may spread out and form sheets, or sheets may fold and form ducts and cavities. As may be appreciated readily, any number of shapes may be produced by moving and rearranging the building blocks.

The net result of growth, differential growth, and form-regulating movements is the elaboration of an organism with distinctly shaped and appropriately sized internal body parts and with a distinct external overall symmetry: spherical, radial, bilateral, or symmetrical. All these aspects of morphogenesis may be said to represent the architectural component of development.

But development includes an important operational component too, and this consists of processes of differentiation. For example, growth of a zygote does not simply produce an aggregate of many identical cells, but an aggregate of mutually different cells: some become nerve cells, some liver cells, some skin cells, etc. Yet all arise from the same protoplasmic mass of the zygote. In every multi-

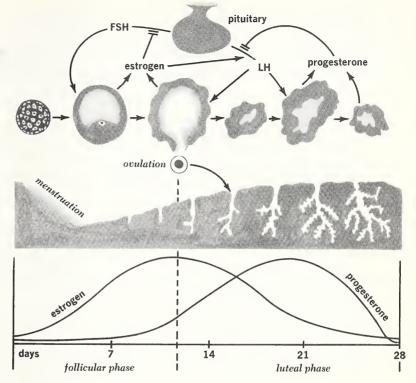


FIG. 21.11. Summary of the menstrual cycle. Top: events in the ovary and the role of the pituitary. Note the gradual growth of the follicle up to ovulation and its subsequent transformation into a corpus luteum. Note also that, just before ovulation, high estrogen concentrations inhibit FSH secretion and also stimulate LH secretion. Falling FSH and rising LH concentrations are the specific trigger for ovulation. Middle: events in the wall of the uterus. Bottom: variations in the amounts of sex hormones during a menstrual cycle.

cellular organism, evidently, the reproductive unit gives rise to a multitude of differently specialized cells. Moreover, most of these cells continue to change their early specializations, repeatedly and in various ways, as development progresses. This holds not only for cells but for every other organizational level as well. Molecules, tissues, organs, whole organisms, all change in character steadily, and indeed it is in large part by this changing that we recognize "development." We say that the parts of a developing organism differentiate, and through this they acquire particular operational capacities, or specializations. A specialized liver cell does not exist

as such in the zygote; rather, the parts of the zygote differentiate, and one result of this may be the gradual emergence of specialized liver cells. Similarly in all other cases.

How does differentiation come about? On the molecular and cellular levels this process is understood only very poorly to date, and indeed it is one of the most crucial unsolved problems in biology. Three general possibilities exist. First, cell differentiation might be a result of progressive changes in gene action. Genes themselves probably do not change, for, as already noted, their stability is an essential requirement for the preservation of species

character. But the *activity* of different genes could vary with time. In a given cell some genes might become active at certain developmental stages whereas other genes might become inactive. Such differential activity patterns might occur differently in different cells, and this might contribute to differentiation.

Or second, gene actions might remain the same but the operations of the cytoplasm could become altered progressively. For example, one round of cytoplasmic reactions might use up a certain set of starting materials, and in the subsequent absence of these, similar reactions could then no longer take place. A next round of reactions would proceed with different starting materials and would therefore produce different endproducts. The net result could be progressive differentiation.

Or third, nuclear and cytoplasmic changes might both occur, in reciprocal fashion. This is probably the likeliest possibility, and much current research is devoted to a study of this very complex key problem. For the present, therefore, we are limited to merely identifying and describing processes of differentiation wherever they occur, without being able to analyze their underlying mechanisms. This is actually true also for all processes of morphogenesis, for here too the underlying mechanisms are

FIG. 21.12. Diagrammatic representation of fertilization. A sperm enters an egg by being engulfed by the egg, through an egg cone which comes to surround the sperm (c). A so-called fertilization membrane lifts off the egg surface after a sperm has made contact. This prevents additional sperms from being engulfed (c and d). The sperm tail is left at the egg surface, and the sperm head (nucleus) alone migrates into the egg cytoplasm, where it fuses with the egg nucleus. An egg is fully fertilized only after sperm and egg nucleus have fused.

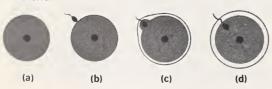




FIG. 21.13. X-ray photo of Siamese twinning in fish. Abnormalities like these result from incomplete divisions of cells during early cleavage. (American Museum of Natural History.)

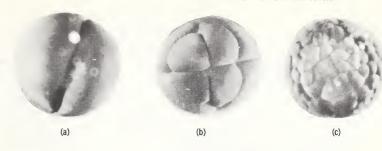
still obscure. What follows represents just such an identification and description of the events of development, specifically as they occur in the transformation of zygotes into multicellular animals.

The process. In all animals, the first event after fertilization (Fig. 21.12) is a series of cell divisions, here called cleavage divisions. Through these, the unicellular zygote becomes a ball of many cells.

We may note here that the occasional formation of *identical twins* fundamentally is an event of cleavage. The zygote divides, and the two resulting cells do not remain together as is normal, but separate. In some animals, each such separate cell then may develop into a whole offspring. If the two cells separate only partially, Siamese twins may be the result (Fig. 21.13). These processes may be duplicated in laboratory experiments, with test animals such as fish, frogs, and others.

The ball of cells produced through normal cleavage is often hollow, one layer of cells forming the wall. Such a stage of development is known as a blastula (Figs. 21.14 and 21.15). Further cell division then occurs, and the blastula undergoes a process of gastrulation. Although the patterns of gastrulation vary widely among animals, the result is always a three-layered embryo known as a gas-

FIG. 21.14. Cleavage in frog eggs. (a) to (c) Two-cell stage, eight-cell stage, and later stage. Note how cell size decreases with successive cleavage divisions. (Carolina Biological Supply Co.)



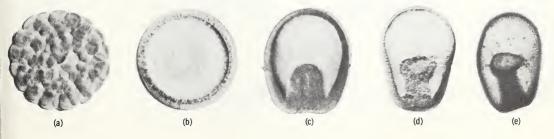
trula. In the superphylum of enterocoelomates, for example, the blastula typically *invaginates*; that is, it becomes dented inward in one area. A two-layered cup-shaped structure is formed in this manner. Of the two layers, the outer is called the *ectoderm* and the inner the *endoderm* (Fig. 21.15). Later a third tissue layer, the *mesoderm*, arises between ectoderm and endoderm. We have already noted in Chap. 9 how the mesoderm forms in the different animal superphyla.

With the development of a gastrula, the broad design of the later mature animal is fairly well established (Fig. 21.16). The ectoderm will give rise to the whole nervous system and the skin, including hair, nails, and skin glands. The mesoderm will form bones, muscles, and the circulatory, excretory, and reproductive systems. The endoderm will produce the alimentary system, the breathing

system, and all glands and ducts associated with these: liver, pancreas, salivary glands, trachea, etc. The opening in the wall of the gastrula, called the blastopore, marks the region of the future anus in enterocoelomates and the region of the future mouth in all other animals. A mouth or an anus will later break through at the opposite end of the gastrula.

The precise ways in which these later transformations occur differ very widely, according to the characteristics of the different animal species. In general, however, all these developmental events involve the outfolding or infolding, the outpouching or inpouching, of portions of the three layers of the gastrula. For example, the nervous system of vertebrates forms by the infolding of a tube of tissue along the dorsal midline of the ectoderm (Fig. 21.17). Later, the eye develops in part as an

FIG. 21.15. The early development of starfish embryos. (a) to (e) Late cleavage; blastula; invagination, early gastrula; late gastrula, beginning of mesoderm formation; mesoderm formation under way. (General Biological Supply House, Inc.)



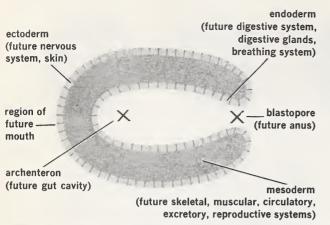


FIG. 21.16. The general structure of a vertebrate gastrula and the adult organ systems formed by each of the primary germ layers (diagrammatic).

outpouching from the forward (i.e., brain) portion of the tubular nervous system. Limbs form by combined localized outpouchings from ectoderm and mesoderm. Lungs and digestive glands develop as outpouching from various levels of the endodermal tube. Analogously for all other organs and body parts. The ultimate result of these folding processes is a fully formed embryo, clearly recognizable as a young stage of a particular species.

Experiments have shown how these orderly sequences of development may come about. Eye development in vertebrates provides a particularly striking example. As just noted above, the formation of an eye starts with the growing out of a pocket from the side of the future brain (Fig. 21.18). This pocket is narrow at the base and bulbous at the tip. Soon the bulbous portion invaginates, or indents, from the forward end, and a double-layered cup is formed. The cup represents the future eyeball. As it grows outward from the brain,

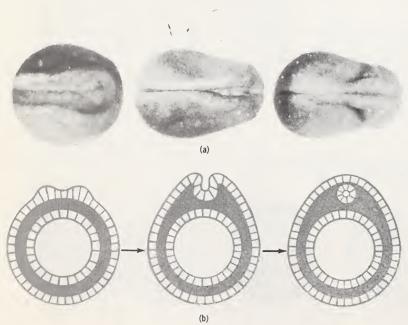


FIG. 21.17. The initial development of the nervous system in vertebrates (frogs). (a) Left to right, dorsal views, progressive stages. The anterior ends of the embryos are toward the right. (b) Diagrammatic cross sections corresponding to the stages shown above. (Photos, Dr. Roberts Rugh, "Experimental Embryology," Burgess Publishing Company, 1948.)

FIG. 21.18. Development of the vertebrate eye (amphibian; semidiagrammatic). This series of successive stages shows the outgrowth of a pocket from the brain, contact of this pocket with the outer body ectoderm, formation of an eyecup, gradual formation of a lens from the outer ectoderm, and development of the pigmented and other tissue layers of the eyeball. (Courtesy of Dr. D. Bodenstein, from originals of figs. 2 and 3, "J. Exptl. Zool.," vol. 108, pp. 96 and 97, by permission.)

its rim comes into contact with the outer ectoderm layer, which, overlying the whole nervous system, represents the future skin. Just where the eyecup rests against it, the ectoderm layer now begins to thicken. This thickening eventually grows into a ball of cells, which is nipped off toward the inside. It fits neatly into the mouth of the eyecup, and it represents the future lens. The cells of this ball and the ectoderm overlying them later become transparent. Thus the basic structure of the eye is established.

The following type of experiment has shown dramatically how this developmental process is controlled. It is possible to cut off the eyecup and its stalk before they have grown very far. Eyecup and stalk may then be transplanted. For example, they may be inserted into a region just under the belly ectoderm of an embryo. Under such conditions, the

patch of belly ectoderm overlying the eyecup soon thickens, a ball of cells is nipped off toward the inside, and a lens matures! Moreover, lens and overlying skin become transparent. In effect, the transplanted structures have caused the formation of a structurally normal eye in a highly abnormal location (Fig. 21.19).

The conclusion to be drawn from this and many similar types of experiments is clear. One tissue layer evidently *interacts* with an adjacent one, and the latter is thereby stimulated to develop in a particular way. This developed tissue then interacts with another one in turn and stimulates it to develop too. One embryonic tissue so functions as a trigger for the development of the next. This general phenomenon has been called embryonic induction. It accounts for the orderly, properly timed, and properly spaced elaboration of body parts.

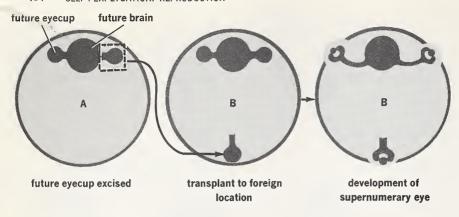




FIG. 21.19. Experiments in eye transplantation. Diagram: if an embryonic eyecup is excised from a donor embryo (A) and is transplanted into an abnormal location in a host embryo (B), then a structurally perfect eye will develop at that abnormal location. Photo: a larva of the amphibian Amblystoma, with two supernumerary eyes grafted into abnormal locations. The procedure followed that outlined in the diagram, and the photo was taken 43 days after the transplant operation. (Photo from original fig. 16, S. R. Detwiler and R. H. Van Dyke, "J. Exptl. Zool.," vol. 69, p.157.)

Embryo and environment

Most animals are aquatic, and their embryos normally develop in natural bodies of water. Enough *yolk* has been stored in the zygote to provide food until the embryo has hatched as larva, with a

functioning alimentary system of its own. But as noted earlier, in most terrestrial animals embryonic development takes place on land, either within protective shells or within the body of the female. In these instances, the developing zygote, as well as the female parent, produces an array of special structures which ensure the survival and proper growth of the young. We may illustrate the nature of these special structures by examining the terrestrial development of reptiles and birds and of mammals.

In reptiles and birds, fertilization is internal and occurs in the oviduct. The zygote becomes enveloped by a calcareous *shell* secreted around it by the oviduct. This shell is porous enough to permit aerial gas exchange, yet not porous enough to permit leakage of water. After the shelled egg is laid and as the zygote within develops, some of the early tissues produced do not become part of the actual embryo. Instead, these tissues form four so-called extraembryonic membranes (Fig. 21.20).

One of these membranes is the chorion. It lies just inside the egg shell and encloses everything within. It prevents undue evaporation of water through the shell. A second membrane, the amnion, surrounds the developing embryo everywhere except on its ventral side. This membrane holds lymphlike

fluid, the amniotic fluid, which bathes the embryo as in a "private pond." The fluid may be regarded as the equivalent of the fresh-water ponds in which the ancestors of reptiles and birds developed. The two remaining membranes pouch out from the ventral side of the embryo, more specifically, from the alimentary tract. One of these is the allantois, which comes to lie against the egg shell, just inside the chorion. Blood vessels ramify through the allantois, and this membrane is the breathing structure of the embryo; gas exchange occurs between it and the air outside the shell. Also, the allantois serves as an embryonic urinary bladder in which metabolic wastes are stored up to the time of hatching. The second membrane on the ventral side is the yolk sac, which contains the ample food stores for development and which gradually gets smaller as the yolk is used up during the growth of the embryo.

In mammals, descended from reptiles, these four extraembryonic membranes are formed in early development too. But they are put to partly new

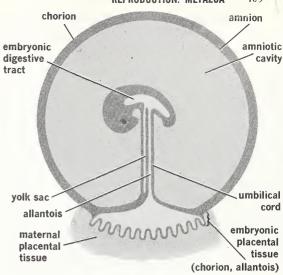


FIG. 21.21. The extraembryonic membranes in mammals and the placenta (diagrammatic). Note that yolk sac and allantois are rudimentary and collapsed.

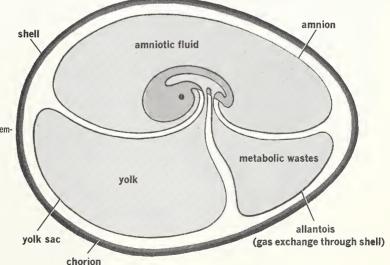
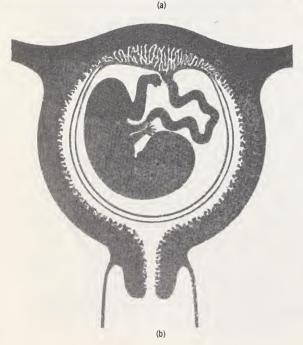


FIG. 21.20. The extraembryonic membranes in reptile and bird eggs.





uses, for the mammalian embryo typically remains within the uterus. First, a shell is not laid down (except in the subclass of egg-laying mammals; see Chap. 9). Second, the outer chorion grows out in one region into fingerlike projections which interlace with the wall of the uterus. This interlacing area is the so-called placenta (Fig. 21.21). It provides a mechanical anchorage holding the embryo attached to the uterus wall. Third, the allantois still functions as an embryonic lung, except that now gas exchange occurs in the placenta, between the embryonic blood vessels of the allantois and the maternal blood vessels of the uterus. The allantois has lost its function as urinary bladder, however, for embryonic wastes are carried off by the maternal blood in the placenta. The allantois is here actually a collapsed, empty sac. This is also true of the yolk sac, for food is now supplied by maternal blood, again through the placenta. We note that the placenta is not only the mechanical, but also the metabolic, link between embryo and mother. Indeed, the allantois and yolk sac together form a umbilical cord, which interconnects embryo and placenta and literally forms a life line (Fig. 21.21 and 21.22). The point of origin of the cord in the embryo leaves a permanent mark in the later offspring in the form of the navel.

The amnion in mammals still has the same function as in reptiles and birds. It is this sac and its fluid which eventually fills and distends the surrounding chorion and uterus and produces the characteristic abdominal enlargement of the pregnant female (Fig. 21.22). At birth, chorion and amnion rupture, the amniotic fluid escapes to the outside, the placenta loosens away from the uterus, and the

FIG. 21.22. (a) Photograph of human embryo, about 8 weeks after fertilization, obtained after surgical removal of portions of the reproductive system of female patient. Chorion pushed to one side, revealing the amniotic sac. Note umbilical cord. (b) Diagram of embryo within its membranes in the uterus; amnion on the inside, chorion on the outside. (Photo by permission, from fig. 10, "The Embryology of Behavior," by Dr. A. Gesell and Harper & Brothers.)

offspring plus umbilical cord plus placenta are expelled. Carnivorous mammals often eat the placenta and the cord (and sometimes the offspring as well). In other cases, these structures soon shrivel, dry out, and break off.

We note that in mammals, and also in reptiles and birds, larval stages are omitted. The embryos develop into adults directly, in smooth growth sequences and without sharp changes in character (Fig. 21.23). Yet larval stages are quite characteristic of fishes and amphibia, ancestral forms of which have given rise to the reptiles, birds, and mammals. This is the general pattern in most animal phyla. The ancestral primitive types generally possessed larvae, and their immediate descendants still do today. However, in more drastically changed descendants of these same ancestors, larval phases are often omitted. But regardless of whether an embryo forms a larva or becomes an adult directly, it ultimately matures into a new individual, in any event, and so leads on to the completion of the entire reproductive process.

This concludes the series of chapters on reproduction. We have found that the extension of protoplasm in space-time is of fundamental importance toward self-perpetuation of life, and we know that, in various ways, genes here exercise a basic controlling role. They direct their own reproduction and also that of all other molecules within cells. And as current research is just now beginning to elucidate, they also direct the development of single reproductive cells into the trillions of ordered, organized, specialized cells which make up any one multicellular organism. With respect to such gene dependence, reproductive and developmental processes do not differ from those of steady-state control.

This brings us directly to the last ingredient of



FIG. 21.23. Stages in the embryonic development of man. Upper left: approximately 25 days after fertilization. Upper right: approximately 33 days after fertilization. Lower left: approximately 6 weeks old. Lower right: approximately 8 weeks old. (Courtesy of Dr. G. W. Corner and Department of Embryology, Carnegie Institution of Washington.)

self-perpetuation, namely, adaptation. For here, even more obviously than in reproduction or in steady-state control, genes are at the root of all happenings too. As they reproduce, these time capsules of protoplasmic tradition become the basis of heredity, and out of heredity is woven the fabric of evolution.

REVIEW QUESTIONS

- 1. Distinguish between external and internal fertilization. In which animals does each occur? After internal fertilization, what happens to the zygotes in different animal groups?
- 2. Review the structure of the reproductive system of human males. Where, specifically, are sperms produced? Describe the hormonal controls of sperm production.
- 3. Review the structure of the reproductive system of human females. Specifically where, and from what tissues, are eggs produced? What is a follicle?
- 4. Describe the hormonal controls and the processes of follicle growth up to the time of ovulation. What events take place during ovulation? After ovulation, what happens to (a) the egg and (b) the follicle?
- 5. Describe the hormonal controls and the events in the uterus up to the time of menstruation. What happens during menstruation? Review the entire menstrual cycle from the standpoint of (a) hormonal control, (b) events in the ovary, and (c) events in the uterus.
 - 6. Describe the location and function of the extraem-

- bryonic membranes in (a) reptiles and birds and (b) mammals. In which vertebrates, and how, is a placenta formed? What are the functions of a placenta?
- 7. Describe, and define, the principal developmental phases in the life history of an organism. What events usually terminate (a) the embryonic period and (b) the larval period?
- 8. What events occur during the cleavage of an egg? Describe the processes leading to the formation of (a) a blastula and (b) a gastrula.
- 9. Define ectoderm, endoderm, mesoderm, blastopore, archenteron. How does mesoderm form in vertebrates? Which structural components of an adult vertebrate develop from each of the three embryonic layers?
- 10. By what general processes do the primary embryonic layers develop into adult structures? Illustrate this in the development of the eye. What role does induction play in such transformations? Describe supporting experiments.

SUGGESTED COLLATERAL READINGS

- Csapo, A.: Progesterone, Sci. American, vol. 198, 1958.
 Dahlberg, G.: An Explanation of Twins, Sci. American, vol. 184, 1951.
- Monroy, A.: Fertilization of the Egg, Sci. American, vol. 183, 1950.
- Moog, F.: Up from the Embryo, Sci. American, vol. 182,
- Pincus, G.: Fertilization in Mammals, Sci. American, vol. 184, 1951.
- Reynolds, S. R. M.: The Umbilical Cord, Sci. American, vol. 187, 1952.
- Rose, S. M.: Transformed Cells, Sci. American, vol. 181, 1949.
- Stone, A.: The Control of Fertility, Sci. American, vol. 190, 1954.
- Waddington, C. H.: How Do Cells Differentiate? Sci. American, vol. 189, 1953.

Part Six

SELF-PERPETUATION: ADAPTATION

On the molecular as on the organismic level, in structure as in function, the living system is adapted to its environment. For example, among thousands of shapes that a fish might possess, it possesses precisely the one which is best suited for rapid locomotion in water. A bird is cast in a form eminently suited for aerial life, yet its ancestry traces to fish. Over long periods of time, clearly, protoplasm may change its particular adaptations, in response to new environments.

Being adapted is a universal attribute of all organisms and all parts of organisms. Adaptation is the long-range process of development which creates and maintains this attribute. Through adaptation, organisms change with their environments, and this makes them potentially immortal as a group.

Based on steady-state control and reproduction, adaptation consists of three components: sex, heredity, and evolution. Of these, the adaptive role of sex has already been discussed earlier. In this last series of chapters, therefore, we begin with an analysis of the adaptive roles of heredity and continue with a similar analysis of evolution. In that connection we shall deal with the mechanism of evolution, that is, the processes through which evolution is believed to occur. And we shall also examine the historical course of evolution, surveying here the array of past organisms which the evolutionary mechanism has created.

CHAPTER 22

Heredity

The key problem in studies of heredity is to explain the inheritance of likeness and of variation: how an offspring usually comes to resemble its parents in certain major respects but differs from the parents in many minor respects. Are such hereditary patterns in any way regular and predictable, and if so, what are the underlying principles?

It should be clear that organisms do not inherit blue eyes, clever minds, red blood, or any other trait. Organisms inherit *genes*, not traits. Visible traits *develop* in an offspring, under the control of inherited genes and within the limitations imposed by given internal and external environments.

Genes cannot be seen, but traits can be. Studies of heredity therefore consist in examining the traits of successive generations of organisms and inferring from the visible likenesses and variations what the heredity of the genes has been. The first important studies of this sort were made in the last half of the nineteenth century by the Austrian monk Gregor Mendel. He discovered two basic rules of inheritance, which laid the foundation for all later advances in understanding processes of heredity.

This discussion of heredity will therefore deal largely with an account of the rules of **Mendelian** inheritance, and with a survey of some of the processes of non-Mendelian inheritance brought to light since the time of Mendel.

GENES AND TRAITS

The pattern of inheritance varies according to whether reproduction is uniparental or biparental. Where an offspring is produced by a single parent, as in vegetative reproduction and in sporulation, the genes of the parent are passed on unchanged to the offspring. In uniparental reproduction, therefore, offspring and parent are genetically identical, and they usually display the same visible traits. In such cases the only source of genetic change, or variation, is mutation. For example, if some gene of an ameba undergoes a mutational change, then, and only then, may the offspring become genetically different from the parent. Trait variations may then be displayed too.

By contrast, two sources of genetic change exist in cases of biparental, i.e., gametic, reproduction. One is again mutation, in this instance mutation in one or both gametes. The other is a direct result of sex. Two sets of genes are pooled in the zygote, and the genetic endowment of the offspring may therefore differ from that of either parent. Through such sexual recombination of genes, the offspring may become unlike the parents.

We conclude, for both uniparental and biparental reproduction, that *likeness* to parents will be inherited to the extent that the genes of the offspring are the same as those of the parents and that *variation* will be inherited to the extent that mutation, sexual recombination, or both have changed the genes of the offspring.

But inheriting a certain gene is not automatically equivalent to developing a certain trait. For the development of traits is affected by the environment. Genes supply a "reasonable promise," as it were, and the total environment of the genes sub-

sequently permits, or does not permit, the translation of promise into reality.

The environment of genes includes, first of all, other genes. Indeed, gene-gene interactions are exceedingly common, as we shall see. The functional integration of genes in a cell is actually so intimate and so complex that it becomes relatively meaningless to speak of "a" gene, as if it were an independent, clearly distinct particle (see also Chap. 16). Only the interacting totality of genes in a cell, called the genome, has functional reality.

The environment of genes also includes the cell cytoplasm, and it too influences the development of traits in major ways. For example, *all* cells of a plant possess flower-color genes, but only cells in the petals express that color. *All* cells of man possess eye-color genes, but only in iris cells does the color become explicit. Evidently, the cytoplasms of different cells are differentially sensitive to the genes they contain, and traits will be expressed differentially as a result (Fig. 22.1).

So-called "inherited" diseases must be interpreted in this light. Certain mental diseases, diabetes, alcoholism, cancer, and many other abnormalities are known to "run in families." What is inherited here is not the disease itself. A child of diabetic ancestry is not automatically diabetic. However, susceptibility to disease may be inherited. The genes are present, but before the disease can become explicit, specific cellular and external environments must make gene expression possible. In a similar vein, a person who performs physical exercise regularly will develop strong muscles and so will acquire traits differing from those of a person who does not exercise. In both cases, however, the genes controlling muscular development may be the same.

We may therefore distinguish between inherited variations of traits, produced by basic genetic differences, and noninherited, acquired variations of traits, produced by environmental or developmental effects. And we are led to the fundamental principle that visible traits are always a product of inherited genes and of environment. To the extent that variations of traits may be advantageous to the organism

in its way of life, heredity, like sex, has adaptive value.

MENDELIAN INHERITANCE

The chromosome theory

In his spare time, Mendel bred and raised several kinds of garden plants, and he kept records of the kinds and numbers of offspring obtained from each mating. He knew, as did others, that a mating of two red-flowered snapdragons, for example, produced exclusively red-flowered offspring. Moreover, all later generations too developed only red flowers. Similarly, a mating of two white-flowered snapdragons yielded exclusively white-flowered progeny in all subsequent generations. Evidently, red and white flower color were true-breeding traits.

It was also well known that when a red-flowered snapdragon was mated with a white-flowered plant, all offspring developed *pink* flowers. In Mendel's time, it was generally supposed that such pinkness resulted from a *blending* of red and white plant pigments, as if paints had been mixed together. Mendel now reasoned that if blending really occurred, pinkness should be true-breeding too, and a mating of two pink-flowered plants should yield pink offspring exclusively.

However, the actual results of such a mating are strikingly different. Two pink-flowered parents consistently produce pink and red and white offspring. Numerically, an average of 50 per cent of the offspring are pink, roughly 25 per cent are red, and the remainder are white. Evidently, pinkness does not breed true, for from pink can be re-created pure red and white, as well as pink. Hence pink color cannot be a permanent blend of red and white (Fig. 22.2).

From data of this kind, Mendel concluded that blending inheritance does not occur and that, instead, traits remain distinct and intact. They may become joined temporarily in one generation and may again become separated, or segregated, from one another in a following generation. This denial

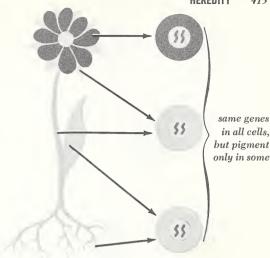


FIG. 22.1. Even though all cells of an organism possess the same kinds of genes, gene action is influenced differently by different cells, resulting in different expression of traits. Thus all cells of a plant may have pigment-producing genes, but actual pigmentation may develop only in the cells of the petals.

of blending was Mendel's most significant contribution. It ultimately reoriented the thinking about heredity completely and paved the way for all modern insights. Mendel himself supplied the first of such insights, for he not only negated the old interpretation but also postulated a new one.

He realized that traits trace back to the sperm and the egg which produce an organism, and he suspected that some specific components within the sperm and the egg controlled the later development of traits. Mendel called these hypothetical components "factors." For any given trait, he argued, an organism must inherit at least one factor from the father and one from the mother. Therefore the offspring must possess at least two factors for each trait. When that offspring in turn becomes a parent, it must similarly contribute *one* factor to its progeny. Hence, at some point before gamete produc-



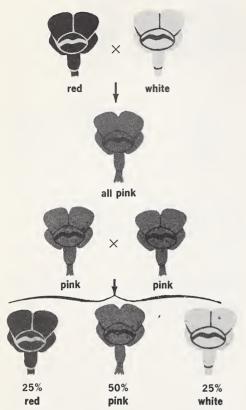


FIG. 22.2. If a red-flowered snapdragon is mated with a white-flowered plant, all offspring will be pink-flowered. And if two of these pink-flowered plants are then mated in turn, the offspring will be red, pink, and white, in the ratios shown.

tion, two factors must be reduced to one. Mendel consequently postulated the existence of a factor-reducing process.

With this he in effect predicted the occurrence of meiosis. When near the end of the nineteenth century meiosis was actually discovered, it was recognized that the reduction of chromosomes matched precisely the postulated reduction of Mendel's factors. Hence chromosomes came to be regarded as the carriers of the factors, and the **chromosome** theory of heredity so emerged. This theory has since received complete confirmation, and Mendel's "factors" became the *genes* of today.

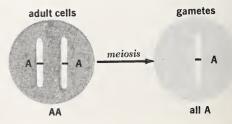
The law of segregation

Transmission of genes. On the basis of the chromosome theory, we may interpret the snapdragon data above as follows. A true-breeding red-flowered plant possesses a pair of red-pigment-producing genes in each cell. These genes, which we may symbolize by the letters AA, are located on a given pair of chromosomes, of which one is maternal and one is paternal in origin. We say that the genotype, or gene content, of the plant is AA and that the phenotype, or visible appearance, is red. Some time before such a plant produces gametes, meiosis occurs. Mature gametes therefore contain only one of the two chromosomes, hence only one of the two genes (Fig. 22.3).

Note that it is entirely a matter of chance which of the two adult chromosomes will become incorporated into a given gamete. Since both adult chromosomes here carry the same color gene, all gametes will be genetically alike in this respect. We may understand now why AA plants are truebreeding, i.e., why a mating of $AA \times AA$ will produce only red-flowered, AA offspring (Fig. 22.4).

In precisely analogous manner, we may symbolize the genotype of a true-breeding white-flowered snap-dragon as *aa*. The letters here represent genes which do not produce any pigment at all: The white

FIG. 22.3



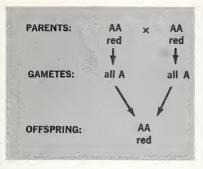


FIG. 22.4

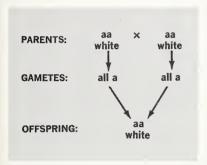
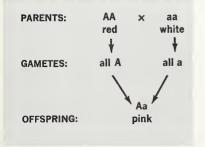


FIG. 22.5

FIG. 22.6



coloration in such flowers is a result of this lack of pigment. A mating of two such plants will yield only white-flowered offspring (Fig. 22.5).

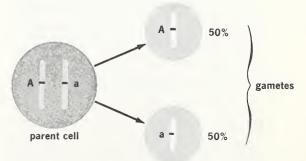
If we now mate a red-flowered and a white-flowered plant, all offspring will be pink (Fig. 22.6).

We may note here that an Aa offspring plant possesses only one pigment-producing gene per cell, namely, A. Such a cell consequently develops only half as much pigment as an AA cell, which possesses two pigment-producing genes. This lesser amount of pigment in the Aa offspring appears as a dilute red, i.e., pink.

If now two pink-flowered Aa plants are mated, meiosis in each plant will give rise to two types of gametes. For, given the genes Aa, either the A gene or the a gene could become incorporated into any given gamete. What actually happens in each specific case is determined by chance. Hence if, as is usually the case in most organisms, large numbers of gametes are produced, each possibility will be realized with roughly equal frequency. Consequently, approximately 50 per cent of the gametes will carry the A gene, the other 50 per cent the a gene. We may write: Aa parent $\rightarrow 50\%$ A gametes, 50% a gametes (Fig. 22.7).

Now fertilization occurs in the $Aa \times Aa$ mating. Each parent produces two genetically different gamete types, and it is wholly a matter of chance which of the two sperm types fertilizes which of the

FIG. 22.7



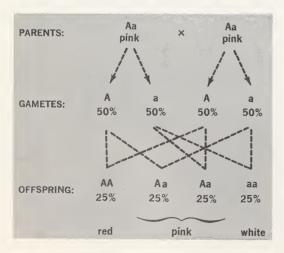
two egg types. If many fertilizations occur simultaneously, as is usually the case, then all possibilities will be realized with appropriate frequency (Fig. 22.8).

We note that half the offspring are pink-flowered and resemble their parents in this respect. One quarter are red-flowered and one quarter white-flowered, and these offspring resemble their grand-parents. We may conclude that the results of Fig. 22.2 can be explained adequately on the basis of nonblending, freely segregating genes and the operations of chance.

Genetic dominance. Genes like A and a, which control the same trait but produce different expressions of that trait, are called *allelic* genes, or alleles. In the snapdragon example above, trait expression evidently depends on the number of A alleles. Presence of A in single dose, as in Aa plants, gives only half as much pigment as presence of A in double dose, as in AA plants. Most traits are affected in this way by gene dosage.

In some cases, however, a maximum trait may be produced even if an allele is present only in single

FIG. 22.8



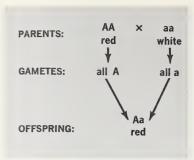


FIG. 22.9

dose. Mendel discovered an instance of this in garden peas. In these, as in snapdragons, true-breeding red-flowered plants may be symbolized as AA, true-breeding white-flowered plants as aa. But when two such plants are mated, all offspring are red, not pink (Fig. 22.9).

Evidently, the single A gene in Aa plants suffices to bring out the full red color, and two A genes, as in AA, do not produce substantially more redness.

Therefore, if two red-flowered Aa plants are mated, three out of every four offspring will be red-flowered (Fig. 22.10).

Genes which produce a maximum trait even when present only in single dose, like the A's of garden peas, are called dominant genes. They mask more or less completely the effect of other alleles, like the a's of garden peas. These latter are called recessive alleles. Offspring in ratios of 3/4: 1/4 are characteristic for matings involving dominant and recessive alleles, as above.

But complete dominance of this sort is far rarer than the allelic relationship illustrated earlier for snapdragons. There the A gene is said to be partially dominant, the a gene partially recessive. Offspring ratios of $\frac{1}{4}:\frac{1}{2}:\frac{1}{4}$ are then characteristic. We may note in this connection that allelic pairs like AA or aa, in which both genes are the same, are called homozygous combinations. By contrast, Aa pairs are called heterozygous combinations. For ex-

ample, an AA genotype in garden peas is said to be "homozygous dominant."

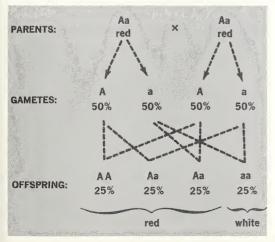
In modern terminology, Mendel's first law, the law of segregation, may now be stated as follows: Genes do not blend, but behave as independent units. They pass intact from one generation to the next, where they may or may not produce visible traits, depending on their dominance characteristics. And genes segregate at random, thereby producing predictable ratios of traits in the offspring. Implied in this law are chromosome reduction by meiosis and the operation of chance in the transmission of genes.

The law of independent assortment

Mendel knew that mature organisms do not express traits one at a time but exhibit all their traits simultaneously. Analogously, we know today that genes are not inherited one at a time, but that all of them are inherited together. Therefore, given certain parents, what will the offspring be like with respect to two or more simultaneous traits?

Mendel discovered a fundamental rule here. Phrased in modern terms, this law of independent

FIG. 22.10



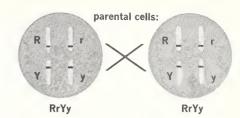


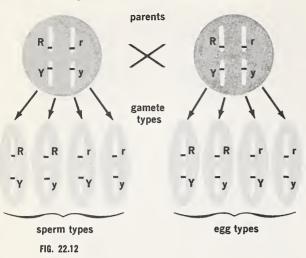
FIG. 22.11

assortment states: The inheritance of a gene pair located on a given chromosome pair is unaffected by the simultaneous inheritance of other gene pairs located on other chromosome pairs. In other words, two or more traits, produced by genes located on two or more chromosome pairs, "assort independently"; that is, each trait will be expressed independently, as if no other traits were present.

Suppose we analyze, as Mendel did, the simultaneous inheritance of two traits of garden peas, seed shape and seed color. Seed shape can be either round or wrinkled. Round can be shown to be dominant over wrinkled, and the possible alleles can be symbolized as R for round and r for wrinkled. Therefore, on a given chromosome pair of peas is located either an RR, an rr, or an Rr pair of alleles. Similarly, yellow seed color (Y) is dominant over green seed color (y). Hence on another chromosome pair is located a YY, or a yy, or a Yy pair of alleles. Let us now mate two RrYy plants, that is, individuals which are heterozygous for both traits. The cells of such parent plants are as in Fig. 22.11.

After meiosis, each gamete will contain only *one* seed-shape gene and only *one* color gene. But which of each pair? The dominant or the recessive gene? This is a matter of chance. There are four possibilities. A gamete might contain the genes R and Y, or R and Y, or R and R, or R and R. Many gametes are produced; hence all four combinations will occur with roughly equal frequency (Fig. 22.12).

Fertilization is governed by chance too. Therefore any one of the four sperm types might fertilize any



one of the four egg types. Hence there are 16 different ways in which fertilization can occur, and if large numbers of fertilizations take place simultaneously, all 16 ways will be realized with roughly equal frequency. We may determine these 16 ways by using a grid where the gametes of one parent are put along a horizontal edge and the gametes of the other parent along a vertical edge (Fig. 22.13).

Among the 16 offspring types here, we find some individuals which contain both dominant genes at least once; some which contain one or the other of the dominant genes at least once; and some which contain none of the dominant genes. A count reveals round-yellow, round-green, wrinkled-yellow, and wrinkled-green to be present in a ratio of 9:3:3:1. This is the ratio Mendel actually obtained and which led him to formulate his law of independent assortment.

For he realized that if seed *shape* is counted alone, there were 9 plus 3, or 12 plants, out of every 16 which were round, and 3 plus 1, or 4 plants, which were wrinkled. But 12:4 is a 3:1 ratio. Similarly, if seed *color* is counted alone, there were again 12 out of every 16 plants which were yellow

and 4 which were green. Here too the ratio is 3:1. Hence, although the shape and color traits both are inherited simultaneously and yield a 9:3:3:1 overall ratio of offspring, each trait considered separately nevertheless gives a 3:1 ratio of offspring. Each trait therefore is inherited as if the other trait were not there at all; or as Mendel put it, the traits "assort independently," each obeying the law of segregation.

Mendel's second law applies specifically to gene pairs located on different chromosome pairs. But any given chromosome contains not just one gene, but anywhere from a few hundred to a few thousand genes. What is the inheritance pattern of two or more gene pairs located on the same chromosome pair? This question leads us beyond Mendel's two laws.

The law of linear order

Genes located within the same chromosomes are said to be linked: as the chromosome is inherited, so are all its genes inherited. Such genes clearly do not assort independently, but they are transmitted together in a block. Hence the traits controlled by linked genes are expressed in a block too. For example, assume that in the heterozygote AaBb the two gene pairs are linked (Fig. 22.14).

When such an organism produces gametes, only two different gamete types are expected, 50 per cent of each (Fig. 22.15).

(We recall that if the gene pairs Aa and Bb were not linked, we should expect four gamete types through independent assortment, namely, AB, ab, Ab, and aB, 25 per cent of each.)

Linkage studies were first undertaken by T. H. Morgan, a renowned American biologist of the early twentieth century. Experimenting with fruit flies, *Drosophila*, Morgan discovered a curious phenomenon. When genes were linked, the expected result of two gamete types in a 50:50 ratio was obtained relatively rarely. Instead, there were usually somewhat fewer than 50 per cent of each gamete type, and there were correspondingly small percentages of two additional, completely unexpected gamete

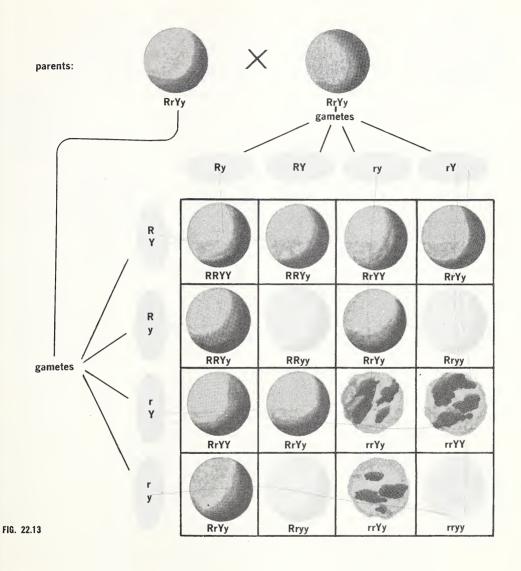


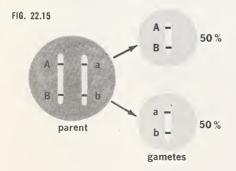


FIG. 22.14

types. For example, instead of obtaining 50 per cent AB and 50 per cent ab gametes, he would obtain, say, only 40 per cent each of AB and ab and, in addition, also 10 per cent each of the unexpected gamete types Ab and aB (Fig. 22.16).

If these four types had formed to an extent of about 25 per cent each, the experiment could have been regarded simply as a case without linkage, governed by Mendel's second law. But the actual results included significantly *more* than 25 per cent each of the expected gamete types and significantly *fewer* than 25 per cent each of the unexpected types.

To explain these odd results, Morgan proposed a new hypothesis. He postulated that during meiosis, paired chromosomes in a few cases might *twist around each other* and might break where twisted, and the broken pieces might fuse again in the "wrong" order (Fig. 22.17).



This could account for the large percentage of expected and the small percentage of unexpected gamete types. To test the validity of this hypothesis, cells undergoing meiosis were examined carefully under the microscope: could chromosome twists and breaks actually be seen? They could indeed, and the phenomenon of crossing over was so proved.

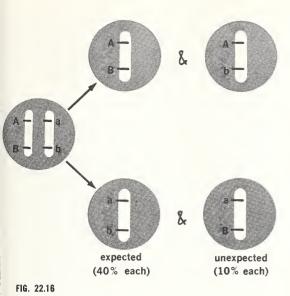
The implications of this discovery were farreaching. It was reasoned that the frequency of crossovers should be an index of the *distance* between two genes. For if two genes on a chromosome are located very near each other, the chances will be relatively small that a twist will occur between these close points. But if two genes are relatively far apart, then twists between these points should be rather frequent. In general, the frequency of crossovers should be proportional to the distance between two genes (Fig. 22.18).

Inasmuch as the crossover percentage of two genes could be determined by breeding experiments, it became possible to construct *gene maps* showing the actual location of given genes on a chromosome. Since Morgan's time, the exact position of a few hundred genes has been mapped in the fruit fly, and smaller numbers of genes have similarly been located in corn among plants and in mice among mammals.

Another implication of crossing over is that genes on a chromosome must be lined up single file. For only if this is the case can linkage and crossing over occur as it actually does occur. This generalization has become known as the law of the linear order of genes, and it constitutes the third major rule which governs Mendelian inheritance.

Finally, crossing over has provided a functional definition of "gene": a gene is the smallest section of a chromosome within which crossovers do not take place. The assumption here is that the minimum chromosome unit able to cross over is one whole gene, not a fractional part of one gene. Recall the two other acceptable definitions of "gene" discussed in Chap. 16.

The three rules of heredity here outlined describe and predict adequately the patterns of Mendelian



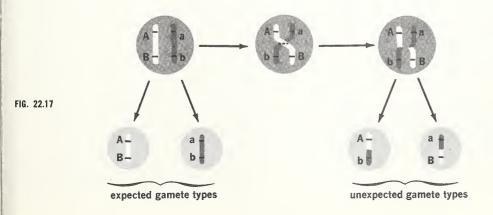
inheritance, that is, the parent-to-offspring transmission of one or more independent gene pairs. But, as noted earlier, genes are not really independent of one another and each one is part of the environment of all the others. Research after the time of Mendel has shown often that genes actually

interact with one another and that a great deal of heredity cannot be accounted for by simply applying the three laws above. In the remainder of this chapter, we shall examine a few instances of such non-Mendelian inheritance.

NON-MENDELIAN INHERITANCE

Gene-gene interactions

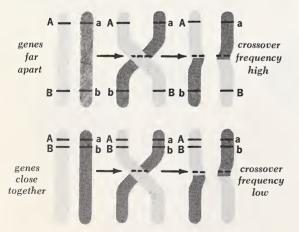
Preoccupation with segregating genes, independently assorting genes, and linearly arranged genes might leave the impression that the units of heredity are simply so many discrete, functionally selfsufficient particles. But if genes were merely independent "beads on a string," haphazardly lined up on given numbers of chromosomes, then it should not matter functionally if the position of genes relative to one another were rearranged. Experiment shows, however, that such rearrangement actually does matter. For example, in Drosophila it is possible to change the position of given sections of a chromosome. A piece lost by one chromosome may become attached to another, or may become reattached to the same chromosome, but in inverted position, or at the other end. Genes here are neither removed from nor added to a cell, and only their position relative to one another is rearranged.



Under such conditions, the cell may nevertheless develop altered traits. Evidently, genes normally interact very subtly with their neighbors, and they are functionally interdependent, not independent.

Many other instances of gene interdependence are known. Partial or complete dominance relationships among alleles are good pertinent examples. Even a completely dominant pigmentproducing gene acts as it does not only because of its inherent characteristics, but also because other genes do not interfere with it, and so permit it to act in dominant fashion. If the functional characteristics of the recessive allele of a given dominant gene were to change, then the status of dominance of that gene would change too. And if the functional characteristics of any other genes in the cell were to change, then the status of dominance of that gene would again change. It is now well established that given gene pairs boost, suppress, partially inhibit, or otherwise modify the effects of other gene pairs. Indeed, it is probable that every

FIG. 22.18. Crossover frequency in relation to gene distance. If two genes are far apart, crossing over between them is likely to occur rather frequently (top). If genes are close together, crossing over between them is less likely. In general, crossing over will be the more frequent the farther apart given genes are on a chromosome.



gene in a cell is a more or less decisive modifier of other genes present. This is understandable if we remember that genes are controllers of metabolic reactions, and other classes of such controllers too are well known to interact with and to affect one another (e.g., hormones).

Thus, whereas the pre-Mendelians thought that traits were inherited, whereas the Mendelian era advanced to the concept that factors, or separate genes, were inherited, the present post-Mendelian era recognizes that actually neither traits nor genes are inherited. Instead, what are inherited are whole chromosome sets, coordinated complexes of genes, subtly integrated genetic systems. And the individual chromosome has emerged as the more significant functional unit of inheritance than the purely conceptual unit we call gene. For what really segregates, assorts independently, and crosses over are chromosomes and parts of chromosomes, not genes.

One case is known which shows particularly well that a complex trait is controlled not so much by separate genes as by whole chromosomes acting as functionally integrated units. The trait in question is sexuality, and its expression provides a good example of non-Mendelian inheritance in general.

Inheritance of sex

In mammals, birds, certain groups of insects, and some other animal types, the primary determiners of sex are chromosomes. These in turn control secondary determiners like sex hormones. In these organisms, the cells of males and females differ with respect to one particular pair of chromosomes. The members of this pair are identifiable by unique shape and size, and they have come to be known as sex chromosomes. For contrast, all other chromosomes are referred to as autosomes. In human cells, for example, there are 22 pairs of autosomes and one pair of sex chromosomes.

In the females of fruit flies and mammals, the two sex chromosomes in each cell are alike; they are called X chromosomes. In males, each cell possesses one X chromosome but the other member

of the pair is visibly different. This member is called the **Y** chromosome (Fig. 22.19). Therefore, in all cells of human *females*,

22 pairs of autosomes plus XX or (44A + XX)

and in all cells of human males,

22 pairs of autosomes plus XY or (44A + XY)

All X chromosomes, like all autosomes, carry genes. The function of Y chromosomes is still rather obscure. They contain but few genes, and the bulk of their substance appears to be genetically inert. Y chromosomes may be lost from cells without appreciable interference with the expression of traits. In effect, therefore, cells of human males contain only 45 functional chromosomes, but female cells contain 46. This difference of one whole X chromosome, with its hundreds of genes, lies at the root of the sexual differences between males and females. In a sense, an X chromosome in its entirety may be regarded as a "gene" for sex.

It can be shown that it is the ratio of autosomes to X chromosomes which is significant in the expression of sex. Autosomes promote the development of maleness, and X chromosomes the development of femaleness. In a human (44A + XX) cell, the total feminizing influence of the two X chromosomes outweighs the total masculinizing influence of the 44 autosomes. Individuals composed of such cells are females. But if the cells contain (44A + XY), then the masculinizing effect of the autosomes is sufficiently strong to override the feminizing effect of the single X chromosome. Such individuals are male.

Hence the sexual nature of certain groups of organisms appears to depend on a particular balance between two genetic influences. If this is correct, should it not be possible to alter the expression of sex by experimentally altering the numerical balance between autosomes and X chromosomes? This is indeed possible. Experiments of this kind actually have given the first clues that chromosome balances play a role in sex determination.

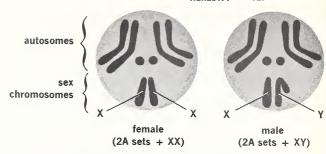


FIG. 22.19. The chromosomes of the fruit fly Drosophila. In each cell, 2n=8. Note the differences in the sex chromosomes of males and females. In man, 2n=46, sex-chromosome differences being as in fruit flies.

In Drosophila, for example, the numbers of autosomes and X chromosomes in sperms and eggs can be varied by certain laboratory procedures. One may then obtain offspring characterized by normal paired sets of autosomes, but by three X chromosomes instead of two. These individuals grow into so-called superfemales: all sexual traits are greatly accentuated in the direction of femaleness. Supermales and intersexes may be produced analogously. In intersexes, sexual traits are intermediate between those of males and females. The chromosome balances are shown in Fig. 22.20. Paradoxically, supersexes, and also intersexes, are generally sterile. For as a result of the abnormal chromosome numbers meiosis occurs abnormally, and the sperms and eggs then produced are defective.

FIG. 22.20. Sex and chromosome balance in the fruit fly. The sexual character of an individual is determined by the specific balance of autosomes and X chromosomes.



superfemale (2A sets + 3X)



intersex (3A sets + 2X)



supermale (3A sets + 1X)

In the light of such balances, we may appreciate readily how the sex of an offspring is inherited normally. Females (44A + XX) give rise to eggs of which each contains (22A + X) after meiosis. Males (44A + XY) produce two kinds of sperms, namely, (22A + X) and (22A + Y), in roughly equal numbers. Fertilization now occurs at random; that is, sperm of either type may unite with an egg. Hence in about 50 per cent of the cases the result will be (22A + X) + (22A + X), or (44A + XX), or a "female" zygote. In the remaining 50 per cent of the cases, the zygotes will be (22A + X) + (22A + Y), or (44A + XY), or "male."

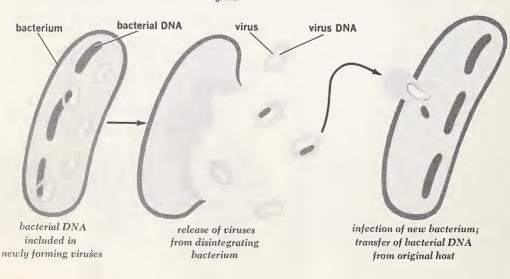
Note that it is the prospective father who, at the moment of fertilization, determines the probable sex of the offspring. When only a single offspring is produced, there exists a 50:50 chance of its being a son or a daughter. When many offspring are produced, the number of males will generally equal the number of females.

Transduction and transformation

To the extent that genetic variations are brought about by the sexual pooling of different chromosomes in the zygote, the pattern is Mendelian and, as we have seen, it obeys the laws of Mendel and Morgan. But inheritable variations may arise also in non-Mendelian fashion.

One rather limited source of such non-Mendelian variations is transduction. This phenomenon was discovered in bacteria, and at the present time it is not known to occur in any other group of organisms. Transduction involves the transfer of genetic material from one bacterium to another, through the agency of particular viruses. These viruses are bacteriophages, that is, they parasitize bacteria (Chap. 4). A virus infects a bacterium and reproduces within the host at the expense of host protoplasm. The host then dies, and the offspring viruses are released, free to infect more bacteria. It happens

FIG. 22.21. The principle of transduction. Newly forming bacteriophage viruses may incorporate into their own structure pieces of the genetic material of the host bacterium. When such viruses infect new bacterial hosts, these hosts acquire additional bacterial genes.



on occasion that bits of the genetic material of a host bacterium become incorporated into newly forming offspring viruses. When the latter subsequently infect new bacterial hosts, they carry the DNA of the old hosts into the new. In this way the new hosts acquire additional hereditary agents and may develop changed or new traits as a result (Fig. 22.21).

Transduction is related in principle to bacterial transformation, another limited source of non-Mendelian variations. This phenomenon has already been referred to briefly in Chap. 16. It is possible by laboratory methods to extract genetic DNA from one strain of bacteria and to expose another strain to the DNA extract. This second strain may then absorb some of the DNA molecules, incorporate them into its own genetic system, and develop new or altered traits as a result (Fig. 16.2). We note that transformation differs from transduction, first, in that a human rather than a viral agency brings about the genetic transfers, and second, in that it is an experimental method of producing variations which, unlike transduction, do not otherwise occur in nature.

Mutation

Transduction and transformation have strictly limited significance. By far the most important source of non-Mendelian variations, of universal significance in all organisms, is mutation. Any stable, inheritable change in the basic genetic system with which every cell is equipped constitutes a mutation. For example, the accidental doubling, tripling, etc., of the normal chromosome number represents a stable, transmissible change. This is a chromosome mutation. Accidental loss or addition of a whole chromosome; loss of a chromosome piece; fusion of such a piece with another chromosome, or fusion with the original chromosome in inverted position, these are chromosome mutations too. They occur on rare occasions in nature, and they may also be produced experimentally.

By far the most common type of mutation is a point mutation, a stable physical and/or chemical

change of one gene (Fig. 22.22). We do not know what produces such mutational gene changes in nature. One possible explanation has emerged from the discovery that high-energy radiation could increase mutation rates. It is now firmly established that the more radiation a cell is exposed to, the more mutations will occur in it. This has suggested that natural mutations might be caused by cosmic rays and other space radiation and by radioactive elements in the earth. However, such unavoidable "background radiation," which affects all organisms, is not sufficiently intense to account for the mutation frequency known to be characteristic of genes generally. This frequency has been estimated as about one mutation per million cells, on the average. To be sure, natural radiation does produce some mutations. Others perhaps represent "errors" in gene reproduction (Chap. 16). And still others are definitely known to be caused by man-made radiation, which adds to, and so increases, the natural background radiation.

As far as can be ascertained, mutations are completely random events. Any gene may mutate at any time, in unpredictable ways. A given gene may mutate several times in rapid succession, then not at all for considerable periods. It may mutate in one direction, then mutate back to its original state or in new directions. There is little question that every gene existing today is a mutant which has undergone many mutations during its past history.

The effect of a mutation on a trait is equally unpredictable. Some are "large" mutations; that is, they affect a major trait in a radical, drastic manner. Others are "small," with but little effect on a trait. Some mutations are dominant, producing immediate positive alterations of traits. Other mutations are recessive and remain masked by normal dominant alleles.

Most mutations are disadvantageous. For inasmuch as a living cell is an exceedingly complex, very finely adjusted whole, it is to be expected that any change of operational character would be more or less disruptive and harmful. In many cases, therefore, dominant mutations tend to be elimi-

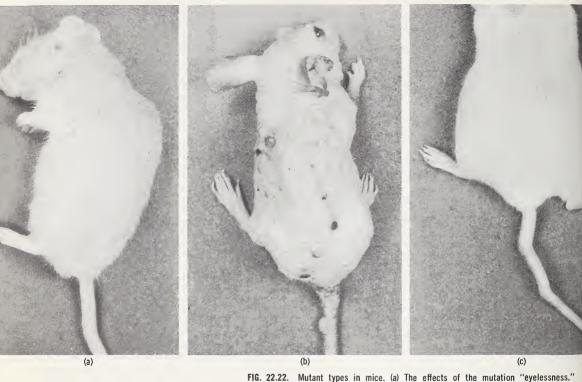


FIG. 22.22. Mutant types in mice. (a) The effects of the mutation "eyelessness." (b) The effects of the mutation "hairlessness." (c) The effects of the "kinky-tail" mutation. Each of these alterations in structure is correlated with a single mutant gene, and the alterations are stable and inheritable. (Courtesy of Dr. H. B. Chase and R. Hughes, Brown University.)

nated as soon as they arise, through death of the affected cell. In other cases, the effect of a dominant mutation, particularly of a "small" dominant mutation, may become integrated successfully into cellular functions, and such a cell, though exhibiting an altered trait, may survive. By and large, however, recessive mutations are likely to persist more readily since their effects may be masked by normal dominant alleles. Accumulated evidence actually shows that most surviving mutations are recessive ones.

A small minority of mutations (probably fewer than 5 per cent) produces advantageous traits and new traits which are neither advantageous nor disadvantageous. Consider mutations in man, for example. Many trillions of cells compose the human body, and mutations occur at an average rate of one in every million cells. Therefore, several million mutations are likely to occur in each person. Many of these may be lethal to the cells in which they occur, and many others will remain masked by normal dominants. But some mutations may pro-

duce traits which do not kill a cell. Such new traits, arising in individual cells, are then transmitted to all cells arising from the original ones by division. For example, "beauty spots" probably develop in this manner.

Gene changes of this type, occurring in body cells generally, are known as somatic mutations. They affect the heredity of the cell progeny, that is, a patch of tissue at most. But in multicellular organisms they have little direct bearing on the heredity of the individual. Entire multicellular offspring are affected only by so-called germ mutations, stable genetic changes in gametes and zygotes. Such mutations are transmitted to all cells composing the off-

spring. In so far as such germ mutations may be recessive and masked by normal dominants, the traits of the offspring will not be altered. But if the offspring is homozygous recessive for a mutation, or if a mutation is dominant, then a particular trait may be expressed in altered form. Provided such a new trait is not lethal, it will persist as an individual variation. We note that mutations may affect the *adaptation* of an individual just as much as the sexual recombination of genes.

And we note that both mutations and sexual recombinations, by bringing about altered adaptations in organisms, are the raw materials of evolution.

REVIEW QUESTIONS

- 1. What are the sources of genetic variation in (a) uniparental, (b) biparental inheritance? Distinguish between inherited and acquired variations. What contributions are made to the expression of traits by (a) genes, (b) the environment? What is an "inherited disease"?
- 2. What was meant by "blending inheritance"? Describe the experiments through which Mendel came to deny blending. What hypothesis did Mendel substitute for the blending concept? State the chromosome theory of heredity. What is the evidence that genes are actually contained within chromosomes?
- **3.** Define: genome, true-breeding, phenotype, genotype, allele, dominant gene, recessive gene, homozygous, heterozygous.
- **4.** In your own words, state the law of segregation. If A is dominant over a, what phenotype ratios of offspring are obtained from the following matings: (a) $Aa \times aa$, (b) $AA \times aa$, (c) $Aa \times Aa$, (d) $Aa \times AA$.
- 5. In your own words, state the law of independent assortment. By what kinds of breeding experiments, and by what reasoning, did Mendel come to discover this law? Interpret the law in terms of genes, meiosis, and gametes.

- 6. Define linkage. Why does inheritance of linked genes not obey Mendel's second law? What were Morgan's observations which led him to the hypothesis of crossing over? Describe this hypothesis. How do crossover data permit the construction of gene maps? State the law of the linear order of genes. What definition of gene is based on the phenomenon of crossing over? Review other definitions.
- 7. Review the genetic basis of sex determination in man. What is the significance of a given numerical balance between autosomes and sex chromosomes?
- 8. What are transduction and transformation? In what organisms, and how, do these processes occur?
- 9. Distinguish between chromosome mutations and point mutations and between somatic mutations and germ mutations. What is the relation between mutation frequency and radiation intensity? What are the characteristics of mutations from the standpoint of (a) predictability, (b) functional relation to normal alleles, (c) effects on traits, and (d) relative advantage to the organism?

SUGGESTED COLLATERAL READINGS

- Flanders, S. E.: Control of Sex in the Honeybee, Sci. Monthly, vol. 71, 1950.
- Hollander, W. F.: Lethal Heredity, Sci. American, vol. 187, 1952.
- Knight, C. A., and D. Fraser: The Mutation of Viruses, Sci. American, vol. 193, 1955.
- Muller, H. J.: Radiation and Human Mutation, Sci. American, vol. 193, 1955.
- Spoerl, E.: The Lethal Effects of Radiation, Sci. American, vol. 185, 1951.
- Stern, C.: Man's Genetic Future, Sci. American, vol. 186, 1952.
- Two or Three Bristles, Am. Scientist, vol. 42, 1954.
- Strong, L. C.: Genetics and Cancer, Sci. American, vol. 183, 1950.

CHAPTER 23

The mechanism of evolution

No one today seriously questions the principle that species arise from preexisting species. For evolution on a small scale can actually be brought about in the laboratory, and the forces which drive and guide evolutionary processes are understood quite thoroughly.

That evolution really occurs did not become definitely established till the nineteenth century. For long ages man was unaware of the process, but he did wonder about the origin of his kind and of other living creatures. Indeed, he developed a succession of simple, rather crude theories about evolu-

tion. Unsupported by good evidence, these were ultimately proved untenable one by one. Yet the early ideas today occasionally still color the views of those who are unacquainted with the modern knowledge.

It is advisable, therefore, that we begin this chapter with a brief survey of the historical background of evolutionary thought. Based on such a perspective, we may then discuss the forces of evolution, as these are understood today, and conclude with an analysis of the nature of evolution, as determined by the underlying forces.

BACKGROUND

Early notions

The earliest theory of organic creation is contained in the Old Testament: God made the world and its living inhabitants in six days, man coming last. On this were based the ideas of *spontaneous generation* and of *immutability* of species, which largely held sway until the eighteenth and nineteenth centuries. Each species was considered to have been created separately, completely developed, from dust, dirt, and other nonliving sources. And once created, a species was held to be immutable, that is, unable to change its characteristics.

In the sixth to fourth centuries B.C., Anaximander, Empedocles, and Aristotle independently considered the possibility that living forms might represent a succession, rather than unrelated, randomly created types. But the succession was thought of in an essentially philosophical way, as a progression from "less nearly perfect" to "more nearly perfect" forms. The historical nature of succession and the continuity of life were not yet recognized. Nor was the notion of continuous succession exploited further in later centuries, for clerical dogma by and large discouraged thinking along such lines.

Francesco Redi, an Italian physician of the seventeenth century, was the first to challenge the idea of spontaneous generation, by showing experimentally that organisms could not arise from nonliving sources. Redi demonstrated, contrary to notions held at the time and earlier, that maggots would never form "spontaneously" in meat if flies were prevented from laying their eggs on the meat. But old beliefs die slowly, and it was not until the nineteenth century, chiefly through the work of Louis Pasteur, that the notion of spontaneous generation finally ceased to be influential.

By this time, the alternative to spontaneous generation, namely, the idea of continuity and historical succession, or *evolution*, had occurred to a number of thinkers. Thus the notion of evolution was clearly

in the air when the nineteenth century began. And in 1809, the first major theory of evolution was actually published. This was the theory of the French biologist Lamarck.

Lamarck

Lamarck considered the reality of evolution as established. To explain how the process occurred, he proposed the two ideas of use and disuse of parts and of inheritance of acquired characteristics. He had observed that if a part of an organism was used extensively, such a part would enlarge and become more efficient. And that if a structure was not fully employed, it would degenerate and atrophy. Therefore, by differential use and disuse of various body parts during its lifetime, an organism would change to some extent and would acquire individual variations. Lamarck then thought that such acquired variations were inheritable and could be transmitted to offspring.

According to this Lamarckian scheme, evolution would come about somewhat as follows. Suppose a given short-necked ancestral animal feeds on tree leaves. As it clears off the lower levels of a tree, it stretches its neck farther up. During a lifetime of stretching, the neck becomes a little longer, and a slightly longer neck therefore is inherited by the offspring. These in turn feed on tree leaves and keep on stretching their necks; and so on, for many generations. Each generation acquires the gains of previous generations and itself adds a little to neck length. In time, a very long-necked animal is formed, for example, something like a modern giraffe.

This theory was exceedingly successful, and it did much to spread the idea of evolution. But Lamarck's views ultimately proved to be untenable. That use and disuse do lead to acquired variations is quite correct. For example, it is common knowledge that much exercise builds big muscles. However, Lamarck was mistaken in assuming that such acquired variations were inheritable. We may say categorically that acquired characteristics are not inheritable. They are effects produced by environment and

development, not by genes. Only genetic characteristics are inheritable, and then only if such characteristics are controlled by the genes of the gametes. What happens to body cells through use and disuse, or in any other way for that matter, does not affect the genes of the gametes. Hence, although Lamarck observed the effects of use and disuse correctly, such effects cannot play a role in evolution.

One famous experimental refutation of Lamarckism was carried out by Weismann, an eminent biologist of the nineteenth century. The tails of mice were cut off for very many successive generations. According to Lamarck, such enforced disuse of tails should eventually lead to tail-less mice. Yet mice in the last generation of the experiment still grew tails as long as their ancestors.

Darwin and Wallace

The year in which Lamarck published his theory was also the year in which Charles Darwin was born. During his early life, Darwin undertook a five-year-long circumglobal voyage as the biologist on the naval expeditionary ship H.M.S. Beagle. He made innumerable observations and collected a large number of specimens of plants and animals, in many parts of the world. Returning home, he spent nearly twenty years sifting and studying the collected data. In the course of this work, he found evidence for certain generalizations. Another biologist, Alfred Wallace, had independently been led to substantially the same generalizations, at the same time as Darwin. Darwin and Wallace together then announced a new theory of evolution which was to supplant that of Lamarck. Darwin subsequently elaborated the new theory into book form. This famous work, entitled "The Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life," was published in 1859.

In essence, the Darwin-Wallace theory of natural selection is based on three observations and on two conclusions drawn from these observations.

Observation: Without environmental pressures,

every species tends to multiply in geometric progression.

In other words, a population doubling its number in a first year possesses a sufficient reproductive potential to quadruple its number in a second year, to increase eightfold in a third year, etc.

Observation: But under field conditions, although fluctuations occur frequently, the size of a population remains remarkably constant over long periods of time.

We have already spoken of this in the discussion of food pyramids (Chap. 4).

Conclusion: Hence not all eggs and sperms will become zygotes, not all zygotes will become adults, and not all adults will survive and reproduce. There must be a "struggle for existence."

Observation: Not all members of a species are alike; that is, there exists considerable individual variation.

Conclusion: Hence in the struggle for existence, individuals featuring favorable variations will enjoy a competitive advantage over others. They will survive in proportionately greater numbers and will produce offspring in proportionately greater numbers.

Darwin and Wallace thus identified the *environment* as the principal cause of natural selection. Through the processes above, the environment would gradually weed out organisms with unfavorable variations but preserve those with favorable variations. Over a long succession of generations and under the continued selective influence of the environment, a group of organisms would eventually have accumulated so many new, favorable variations that a new species would in effect have arisen from the ancestral stock.

Nonbiologists today often are under the impression that the Darwin-Wallace theory is the modern theory of evolution. This is not the case. Indeed, Darwinism was challenged even during Darwin's lifetime. What, it was asked, is the source of the all-important individual variations? How do individual variations arise? Here Darwin actually could

do no better than fall back on the Lamarckian idea of inheritance of acquired characteristics. Ironically, the correct answer regarding variations began to be formulated just six years after Darwin published his theory, when a monk named Mendel announced certain rules of inheritance! But the significance of Mendel's work was not appreciated for more than thirty years, and progress in understanding evolutionary mechanisms was correspondingly retarded.

Another objection to Darwinism concerned natural selection itself. If this process simply preserves or weeds out what already exists, it was asked, how can it ever create anything new? As we shall see, natural selection actually does create novelty, and the earlier criticism arose in part because the meaning of Darwin's theory was-and still is-widely misinterpreted. Social philosophers of the time and other "press agents" and disseminators of "news," not biologists, thought that the essence of natural selection was described by the phrase "struggle for existence"; and they coined alternative slogans like "survival of the fittest" and "elimination of the unfit." Natural selection so came to be conceived almost exclusively as a negative, destructive force, and this had two unfortunate results. First, a major implication of Darwin's theory, namely, the creative role of natural selection, was missed, and second, the wrong emphasis was often accepted in popular thinking as the last and final word concerning evolution.

Such thinking proceeded in high gear even in Darwin's day. Many still did not accept the reality of evolution and were prompted variously to debate, to scorn, and to ridicule the merits of the evidence. It was felt also (quite without basis) that evolution implied "Man descended from the apes," and man's sense of superiority was duly outraged. Moreover, because evolutionary views denied the special creation of man, they were widely held to be antireligious. In actuality, the idea of evolution is not any more or any less antireligious than the idea of special creation, for neither really strengthens, weakens, or otherwise affects belief in God. To the

religious person, only the way God operates, not God as such, is in question.

But many were properly convinced by the evidence for evolution. However, under the banner of phrases like "survival of the fittest," evolution was interpreted to prove an essential cruelty of nature, and human behavior, personal and national, often came to be guided by the ethic of "jungle law," "might is right," "every man for himself." Only in that way, it was thought could the "fittest" prevail. Even today, unfortunately, evolution is still commonly—and erroneously—thought to be a matter of "survival of the fittest."

By now, more than a full century after Darwin and Wallace, the emotion-charged atmosphere has cleared and the impact of their theory may be assessed calmly. That Darwin made the greater contribution cannot be questioned. In voluminous writings, he, far more than Wallace, marshaled the evidence for the occurrence of evolution so extensively and so well that the reality of the process has never been in doubt since. Moreover, the theory of natural selection was the most convincing explanation of the evolutionary mechanism offered up to that time. Indeed, carrying new meaning today, it still forms a part of the modern theory of evolution. As now understood, however, natural selection is preeminently a peaceful process, and it has almost nothing to do with "struggle," "weeding out," or "the fittest." Also, we know that Darwin and Wallace, like Lamarck, were unsuccessful in identifying the actual sources of individual variations. In short, Darwin and Wallace supplied an incomplete explanation, but as far as it went, theirs was the first to point in the right direction.

The modern theory of evolution is not the work of any one man, and it did not arise by "special creation," fully developed. Rather, it evolved slowly during the first half of the current century, many biologists of various specializations contributing to it. The theory is the spiritual offspring of Mendel and of Darwin, but the family resemblance, though present, may not be immediately evident. We shall

be concerned with this modern theory in what follows.

THE FORCES OF EVOLUTION

The evolutionary process

The medium of evolution is the *population*. The raw materials of the evolutionary process are the *inheritable variations* which appear among the individuals of a population. And the mechanism of evolution may be described as natural selection acting on the inheritable variations of a population.

We already know from Chap. 4 that a population is a geographically localized group of organisms of the same species in which the members interbreed preferentially with one another and also interbreed occasionally with members of neighboring populations. We may note now that the result of the close sexual communication within a population is a free flow of genes. Hereditary material present in a part of a population may in time spread to the whole population, through the genepooling and gene-combining effect of sex. Therefore, in the course of successive sexual generations, the total genetic content of a population may become shuffled and reshuffled thoroughly. We may say that a population possesses a given gene pool and that the interbreeding members of the population have free access to all components of that pool. Moreover, inasmuch as sister populations are in occasional reproductive contact, the gene pool of one population is connected also to the gene pools of sister populations. In this way, the total genetic content of an entire species continues to be shuffled about among the member organisms (Fig. 23.1).

Evolution operates via the gene pools of populations. We already know from Chap. 22 how changes in genetic systems, hence inheritable variations, may arise: by sexual recombination and by mutation. In each generation, some individuals may appear featuring new trait variations, as a result of either recombinational or mutational processes. If

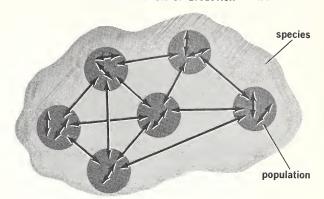


FIG. 23.1. The concept of "gene pool." In a species, gene flow occurs within and between populations. The total gene content of the species thus represents a gene pool to which all members of the species have access. Gene flow cannot occur between the gene pools of two different species.

these variant organisms survive and have offspring of their own, then their particular genetic innovations will persist in the gene pool of the population. And in the course of successive generations, the genetic novelty may spread to many or all members of the population.

Whether or not such spreading actually takes place depends on natural selection. This term is synonymous with differential reproduction, and either "natural selection" or "differential reproduction" means simply that some individuals of a population have more offspring than others. Clearly, those which leave more offspring will contribute a proportionately greater percentage of individuals to the numerical total of the next generation than those which leave fewer offspring. Hence if differential reproduction continues in the same manner over many generations, the abundant reproducers will contribute a progressively larger number of individuals to the whole population. As a result, their genes will become preponderant in the gene pool of the population (Fig. 23.2).

434

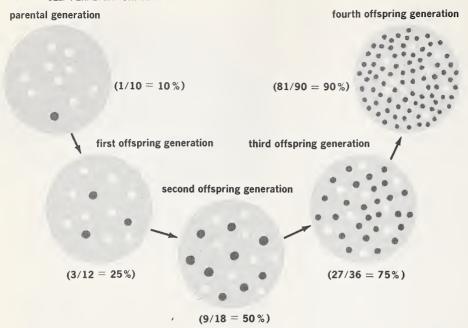


FIG. 23.2. The effect of differential reproduction or natural selection. Assume that a variation arises in one individual of a parental generation (black dot) and that such variant organisms are able to leave three offspring. Each nonvariant organism (white dot), on the other hand, manages to leave one offspring only. The complexion of the population will then change as shown during subsequent generations; i.e., the variant type will represent a progressively larger fraction of the numerical total. Such spreading of variations, brought about by differential reproduction, constitutes natural selection.

Which individuals leave more offspring than others? Usually, but by no means necessarily, those that are best adapted to the environment. Being well adapted, such individuals on the whole are healthier and better fed, may find mates more readily, and may care for their offspring appropriately. However, circumstances may on occasion be such that comparatively poorly adapted individuals have the most offspring. Instances of this are sometimes encountered in human populations, for example. In any event, what counts in evolution is not how well or how poorly an organism copes with its environment, but only how many off-

spring it manages to leave. The more there are, the greater a role will the parental genes play in the total genetic content of the population. By and large, the well-adapted organism contributes most to the gene pool.

Hence, if an inheritable variation appears in an organism and if, through differential reproduction in successive generations, the progeny of that organism becomes numerically more and more abundant, then a given genetic novelty will spread rapidly throughout the population. As a result, a trait variation originating in one organism will have become a standard feature of the population as a whole.

This is the unit of evolutionary change. Many such unit changes must accumulate in a population before the organisms are sufficiently altered in structure or function to be established as a new species. All evolution operates through the basic process just described. In brief, it consists of:

- (1) Appearance of inheritable variations by sexual recombination and mutation
- (2) Spreading of these variations through a population, by differential reproduction in successive generations

Inasmuch as inheritable variations originate at random, evolutionary innovations too appear at random. And inasmuch as the best reproducers are generally the best adapted, evolution as a whole is directed by adaptation and is oriented toward continued or improved adaptation.

Note that, in this modern view of evolution, natural selection is fundamentally a creative force, for its important effect is to spread genetic novelty, hence new traits, through a population. It is also a peaceful force, involving reproduction, not "struggle for existence" or "survival of the fittest." Organisms actually struggle rather rarely. Indeed, they try to avoid struggle and attempt to pursue life as inconspicuously as possible, eating when they can, reproducing when they can. Moreover, natural selection does not "eliminate the unfit." The "fit" may be the mightiest and grandest organism in the population, but it might happen to be sterile. And the "unfit" could be a sickly weakling, yet have numerous offspring. The point is that neither "survival" nor "elimination" is actually at issue. The only issue of consequence here is comparative reproductive success. Indirectly, to be sure, health, fitness, and even actual physical struggles may affect the reproductive success of organisms. To that extent such factors can have evolutionary consequences. But what in Darwin's day was regarded as the whole of natural selection is now clearly recognized to have only a limited, indirect effect on evolution. The whole of natural selection, directly and indirectly, undoubtedly is differential reproduction.

The genetic basis

From the preceding, we may describe evolution as a progressive change of gene frequencies. This means that in the course of successive generations, the proportion of some genes in the population increases and the proportion of others decreases. For example, a mutation may at first be represented by a single gene, but if by natural selection this mutation spreads to more and more individuals, then its frequency increases, whereas the frequency of the original, unmutated gene decreases. Clearly, the *rates* with which gene frequencies change will be a measure of the speed of evolution. What determines such rates?

By experiment and calculation, it can be shown that if mating is random, if mutations do not occur, and if the population is large, then gene frequencies in a population remain constant from generation to generation. This generalization is known as the Hardy-Weinberg law. It is to the theory of evolution what Mendel's laws are to the theory of heredity.

The Hardy-Weinberg law indicates that when a population is in 'genetic equilibrium, i.e., when gene frequencies do not change, then the rate of evolution is zero; that is, genes continue to be reshuffled by sexual recombination, and as a result, individual variations continue to originate from this source. But the overall gene frequencies do not change, and of themselves, therefore, the variations are *not* being propagated differentially. Evolution consequently does not occur.

What does make evolution occur are deviations from the "ifs" specified in the Hardy-Weinberg law. First, mating is decidedly not random in most natural situations. For mates most often are deliberately chosen on the basis of health, strength, mentality, external appearance, or some other desirable traits. By and large, "desirable" traits are those which are adaptive, that is, which promise aid in survival. When two individuals with mutually desirable traits mate, this means that their genes, which control their traits, will increase in numbers through offspring and will spread through the

population. By contrast, two individuals with mutually undesirable traits will not mate, and their genes therefore cannot spread. Thus nonrandom mating in a population means natural selection and uneven, nonrandom shuffling about of genes. Consequently, as some genes spread more than others, gene frequencies will become altered. Hence a Hardy-Weinberg equilibrium will not be maintained. This represents evolutionary change. We say that a certain intensity of natural selection, or selection pressure, operates for or against given genes. In the course of many generations, even a very slight selection pressure affects the genetic make-up of a population substantially.

Second, mutations do occur in populations, and Hardy-Weinberg equilibria change for this reason also. It will be readily appreciated that, depending on whether a mutation produces a desirable or an undesirable trait, the mutated gene will be selected for or against. In either case, gene frequencies will change, since the mutated gene will either increase or decrease in abundance.

We may note here that the evolutionary effect of mutations varies according to whether the gene changes are dominant or recessive. A newly originated dominant mutation will affect traits immediately, and selection for or against it will take place at once. But if a mutation is recessive, it does not affect traits immediately. Hence natural selection does not influence it immediately either. This is the case with most mutations since, as noted in Chap. 22, most actual mutations are recessive.

Nevertheless, recessive mutations may spread through a population. For example, an organism may carry a recessive mutant gene a', and it may also carry a dominant gene B, which produces an adaptively very desirable trait. Natural selection will then operate for the gene B; that is, the organism possessing B will reproduce abundantly. This means that not only B, but also the mutant gene a', will spread through the population. Many recessive mutations actually do propagate in this way, by being inherited along with other, adaptively useful dominant genes.

Recessive mutants simply accumulate in the gene pool, without visible effect. However, if two individuals carrying the same recessive mutation happen to mate, then one-fourth of their offspring will be homozygous recessive: $Aa' \times Aa' \rightarrow 25\%$ a'a'. These offspring will feature altered visible traits, and natural selection will then affect the mutation directly.

Mutational effects in evolution also vary according to how greatly a given mutation influences a given trait. A "large" mutation, affecting a vital trait in major ways, is likely to be exceedingly harmful and will usually be lethal. For example, any change in the principal structure and function of the human heart is likely to cause immediate death. Indeed, large variations are usually eliminated as soon as they arise. By contrast, an organism may survive far more readily if a mutation is "small." Evolutionary alterations of organisms actually occur almost exclusively through the accumulation of many, small changes in traits, not through single, large changes.

The third condition affecting Hardy-Weinberg equilibria is population size. If a population is large, any regional imbalances of gene frequencies, arising by chance, are quickly smoothed out by the many random matings among the many individuals. The principle underlying this holds in statistical systems generally. In a coin-flipping experiment, for example, "heads" and "tails" will each come up 50 per cent of the time, but only if the number of throws is large. If only three or four throws are made, it is quite possible that all will come up heads, by chance alone. Analogously, gene combinations attain Hardy-Weinberg equilibria only if a population is large. In small groups, chance alone may produce major deviations. We say that, in small populations, chance leads to genetic drift, that is, to the random establishment of genetic types which numerically are not in accordance with Hardy-Weinberg equilibria. Because genetic drift is governed solely by chance, natural selection plays little role. Genes here are being propagated, not for their adaptive value, but because they happen to be

picked for progagation by chance. The result is that, in small populations, nonadaptive, often bizarre traits become established, which may actually be harmful to the population and may promote its getting even smaller. Genetic drift is often observed among plants and animals on islands and in other small, reproductively isolated groups of organisms.

Evolution as it actually occurs must be interpreted in terms of the forces here described. That it in fact can be interpreted on this basis will become clear in the following.

THE NATURE OF EVOLUTION

Speciation

The key process to be explained is how unit evolutionary changes in a population eventually culminate in the origin of new species and higher taxonomic categories. A species, we recall, is a collection of populations within which reproductive communication is maintained by interbreeding. We may now define a species alternatively as a group of populations sharing the same gene pool. Within the pool a free flow of genes is maintained, but genetic flow between two such pools does not occur; a reproductive barrier isolates one species from another. The problem of speciation, therefore, is to show how reproductive barriers arise.

We have already discussed this in Chap. 4, and it is advisable for present purposes to reread the section on speciation in that chapter. In brief, we have found that physical distance between two sister populations, and other geographical isolating conditions, usually are the primary causes for an interruption of gene flow. To the geographical barriers then are added biological ones, through the gradual accumulation of evolutionary differences in the different populations. As a result, two populations do not interbreed even though at first they still could, and in time they become so different that they can no longer interbreed at all. Gene flow is then interrupted irreversibly. What started out as

two populations of the same species has become two distinct and separate species.

Consciously or unconsciously making use of this principle of reproductive isolation, man has been, and is now, contributing to the evolution of many other organisms. Here may be found direct proof that evolution actually occurs and, indeed, that it operates according to the mechanism described above.

The most ancient evolution-directing effort of man is his successful domestication of various plants and animals. Darwin was the first to recognize the theoretical significance of domestication, and it was this, actually, which led him to his concept of natural selection. He reasoned that if man, by artificial selection and isolation, can transform wild varieties of given plants and animals into domesticated varieties, then perhaps natural selection and isolation, acting for far longer periods, can bring about even greater evolutionary transformations in nature. We know now that the domesticating process in fact does involve all the elements of natural evolution: first, deliberate physical, hence reproductive and genetic, isolation of a wild population by man; and second, long-continued, carefully controlled, differential reproduction of individuals "adapted" to human desires, i.e., of individuals featuring traits considered desirable by man. The result is the creation of new strains, races, subspecies, and even species (Fig. 23.3).

Furthermore, during the last few decades, rather rapid, man-directed evolution has taken place among certain viruses, bacteria, insects, various parasites, and other pest organisms. These live now in an environment in which antibiotics and numerous pest-killing drugs have become distinct hazards. And the organisms have evolved, and are still evolving, increasing resistance to such drugs. Indeed, the very rapid evolution of viruses and bacteria becomes a problem in research. For laboratory populations of microorganisms may evolve resistance to a drug even while the drug is being tested. Because microorganisms have exceedingly short generation times, because their populations are physically



FIG. 23.3. Red jungle fowl; an example of a wild animal from which man has bred domesticated varieties by artificial selection. (New York Zoological Society.)

small, compact, and easily reared, and because high mutation rates may be induced readily by X rays, they have become favorite test objects in evolution experiments.

Clearly, then, small-scale evolution unquestionably occurs and is observable directly. Moreover, it may be made to occur under conditions based on the postulated modern mechanism of evolution. That this mechanism actually operates as implied by theory is therefore no longer in doubt.

And we may note that the same mechanism is believed to operate in the transformation of species into genera, families, and other higher taxonomic categories. Creation of such a category out of a species is again envisaged to involve isolation and accumulation of small inheritable-trait variations—

only more of them than in the case of a species, and accumulating for a longer period of time.

Characteristics of evolution

Rates of change. Even on the species level, evolution is an exceedingly slow process. As noted, a very large number of very small variations of traits must accumulate, bit by bit over many generations, before a significant structural or functional alteration of organisms is in evidence. Moreover, genetic innovations occur at random, whereas natural selection is directed by adaptation. Hence, if a substantial environmental change necessitates a correspondingly substantial adaptive change in a group of organisms, then the organisms must await the random appearance of appropriate genetic innovations. If useful innovations do not happen to arise by chance, then the organisms will not be able to readapt and will die out. Yet even if useful genetic novelty does arise in a given generation, there is no guarantee that more novelty of similar usefulness will originate in the next generation. In short, even though evolution may occur, it could occur too slowly to permit successful adaptation to changed environments.

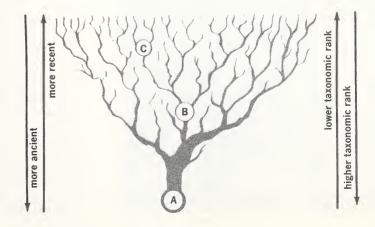
The actual speeds of past evolution, though slow in all instances, have varied considerably for different types of organisms, differently at different times. As a rule, the more stable a given environment has been, the slower has been the evolution of the organisms living in it. Thus terrestrial organisms by and large have evolved faster than marine organisms. Also, during periods of major geologic upheavals, e.g., in times of glaciation or of mountain building (Chap. 24), evolution has been fairly rapid generally. On the other hand, in a few existing animal types, the rate of evolution has been practically zero for hundreds of millions of years. Horseshoe crabs, certain lampshells, and radiolarian protozoa are among the oldest of such "living fossils" (Fig. 9.27). In these and similar cases, the specific environment of the organisms has been stable enough to make the ancient way of life still possible. Given the general evolutionary mechanism of small random variations acted on by adaptively oriented natural selection, it is not surprising that speeds of evolution should have varied in step with environmental changes.

Adaptive radiation. A general feature of evolution is the phenomenon of adaptive radiation. We have seen how, in speciation, one original parent species gives rise simultaneously to two or more descendant species. A similar pattern of branching descent characterizes evolution on all levels. A new type evolves, and it then becomes a potential ancestor for many different, simultaneous descendant lines. For example, the ancestral mammalian type has given rise simultaneously to several lines of grazing plains animals (e.g., horses, cattle, goats), to burrowing animals (e.g., moles), to flying animals (e.g., bats), to several lines of aquatic animals (e.g., whales, seals, sea cows), to animals living in trees (e.g., monkeys), to carnivorous predators (e.g., dogs, cats), and to many others. Evidently the original mammalian type branched out and exploited many different available environments and ways of life. Each descendant line thereby became adaptively specialized in a particular way, and the sum of the various lines, all leading away from the common ancestral type, formed an "adaptive radiation."

Within each such line, furthermore, adaptive radiations of smaller scope can take place. For example, the line of tree-living mammals in time evolved several simultaneous sublines, and each of these in turn gave rise to subsublines, etc. The specific results today are animals as varied as monkeys, lemurs, tarsiers, apes, and men. Evidently, man did not "descend from the apes." Rather, apes and man have had a common ancestor, and they are *contemporary* members of the same adaptive radiation.

The important implication here is that evolution is *not* a "ladder" or a "scale." The pattern is more nearly that of a greatly branching bush, where the tips of all uppermost branches represent currently living species (Fig. 23.4). Of these, none is "higher" or "lower" than any other. Instead, they are simply contemporary groups of different structure, function, and history. And as already pointed out in Chap. 7, the all-too-frequent picture of evolution as a "progression from ameba to man" is, and always has been, utterly without foundation. Leading down from the branch tips to progressively thicker branches, the evolutionary bush goes backward in

FIG. 23.4. The bush pattern of evolution. The uppermost tips of the branches represent currently living forms, and branches terminating below the top represent extinct forms. Fork points such as B and C are ancestral types. B is more ancient and of higher taxonomic rank than C. A represents the archancestor of all living types.



time. Junctions of branches represent common ancestors, and these are the higher in taxonomic rank the more closely the main stem is approached.

Extinction. Not all the branches on a bush ramify right to the top, but some terminate abruptly at various intermediate points. In evolution too, extinction is a general feature. In many cases of extinction, the specific causes may never be known.

FIG. 23.5. An animal which has become extinct relatively recently. The dodo survived till just a few hundred years ago. (American Museum of Natural History.)



But the general cause of all extinctions emerges from the nature of the evolutionary mechanism. That cause is change in environment, without rapid enough readaptation of organisms to the change. Evidently, unlike death, which is inherent in the life history of every individual, extinction is *not* a foregone conclusion inherent in the evolutionary history of every group. Rather, extinction occurs only if and when the group cannot make adaptive adjustments to environmental change (Fig. 23.5).

Such change need not necessarily be physical. For example, biological competition between two different types occupying the same territory often has led to the extinction of one. However, note that competition most often does not involve direct combat or "struggle." Characteristically, the competition is usually quite indirect, as when two different types of herbivores draw on the same limited supply of grass.

In past evolution, extinction has been the more common the lower the taxonomic category. Extinction of species, and even of genera, has been a nearly universal occurrence, but relatively few orders and still fewer classes have become extinct. And practically all phyla that ever originated continue to be in existence today. The phylum evidently includes so broad and so far-flung an assemblage of different adaptive types that at least some of them have always persisted, regardless of how environments have changed. Species, on the other hand, are usually adapted rather narrowly to limited, circumscribed environments, and the chances for extinction are therefore greater.

Replacement. In conjunction with extinction, replacement is another common occurrence in evolution. As noted, competition may be a direct cause of the replacement of one group in a given environment by another. For example, pouched marsupial mammals were very abundant in the Americas a few million years ago, but with the exception of forms like the opossum, they were replaced in the Western Hemisphere by the competing placental mammals. Competition is not a necessary prerequi-

site for replacement, however. A group may become extinct for some other reason, and another group may then evolve into the vacated environment and way of life. A good example of this is provided by the ichthyosaurs. These large, marine, fishlike reptiles became extinct some 100 million years ago, and their particular mode of living subsequently remained unused for about 40 million years. Dolphins and porpoises evolved then, and these mammals replaced the ichthyosaurs. Similar replacement occurred between the flying reptilian pterosaurs and the later mammalian bats (Fig. 23.6).

Convergence and divergence. The phenomenon of replacement is often accompanied by that of convergence, a frequent feature in evolution generally. We have seen how, in an adaptive radiation, a common ancestral type gives rise to two or more descendant lines, all adapted in different ways to different environments. Such development of dissimilar characteristics in closely related groups is often called evolutionary divergence. By contrast, when two or more unrelated groups adapt to the same type of environment, then their evolution is oriented in the same direction. Such organisms may come to resemble one another in one or more ways. Evolution of a common set of characteristics in groups of different ancestry is called convergence (Fig. 23.7).

For example, the development of wings in both pterosaurs and bats, or of finlike appendages in both ichthyosaurs and dolphins, illustrates evolutionary convergence in replacing forms. Inasmuch as the replacing type adopts a way of life similar to that of the type which is being replaced, the appearance of convergent features is not surprising. But convergence is also encountered in nonreplacing forms. For example, the eyes of squids and of fish are remarkably alike. Squids and fish are not related directly, and neither replaces the other. However, both groups comprise large, fast swimmers, and good eyes of a particular construction are a distinct advantage in the ways of life of both. Selection actually has promoted variations which

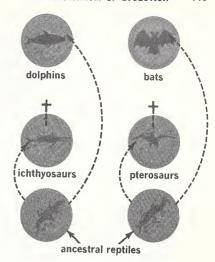


FIG. 23.6. Diagrams of evolutionary replacement.

have led to eyes of similar structure, and the observed convergence is the result.

Opportunism. We may note that although the eyes of squids and fish are strikingly alike, they are by no means identical. Similarly, although the wings of pterosaurs and bats, and also of insects and birds, are convergent, in the sense that all carry out the same functions of flying, the various wing types are quite different structurally and they operate in different ways. Convergence leads to similarity, never to identity. Moreover, neither squids nor fish possess a theoretically "best" eye structure for fast swimmers, and none of the flying groups possesses a theoretically "best" wing design. Engineering specialists in optics and aviation can probably point out numerous operational imperfections in all these organs and can design devices for vision or flight which are theoretically far more efficient.

The point is that eyes, wings, or any other structures need not be theoretically best. They only need to be *practically workable*. In a way of life based

DIVERGENCE

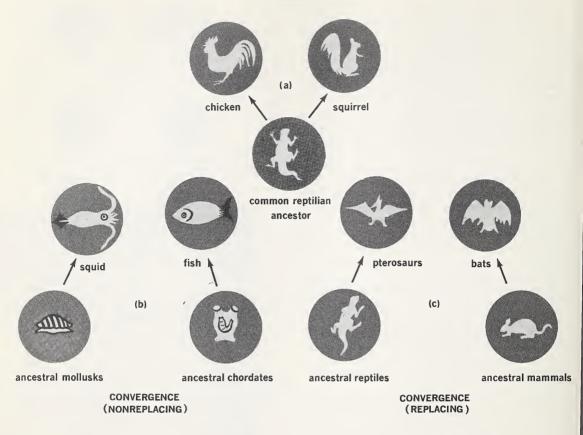


FIG. 23.7. In evolutionary divergence (a), a common ancestor gives rise to different descendant lines. In evolutionary convergence (b) and (c), relatively unrelated ancestors give rise to rather similar lines.

on flying, wings of *some* sort are clearly essential. But virtually all requirements for living can have *multiple* solutions, and so long as a given solution works at all, it does not matter how the solution is arrived at. The various animal wings do represent multiple solutions of the same problem, each

evolved from a different starting point and each functioning in a different way. Similarly for all other instances of evolutionary convergence.

We are led to one of the most important and most universal characteristics of evolution, that of random opportunism. Evolution has produced not

what is theoretically desirable or best, but what is practically possible. There has been no predetermined plan, no striving for set "goals," but only the exploitation of actually available opportunities offered by selection among random hereditary changes. For example, it might have been adaptively exceedingly useful for terrestrial plants to grow legs, or for terrestrial animals to grow wheels. But neither occurred, because it could not occur. The ancestors in each case simply did not possess the necessary structural and functional potential. However, they did possess the potential to evolve adequate, workable, alternative solutions. In the case of plants, already existing spores could be distributed by wind, and in the case of animals, already existing fins could be reshaped into walking legs.

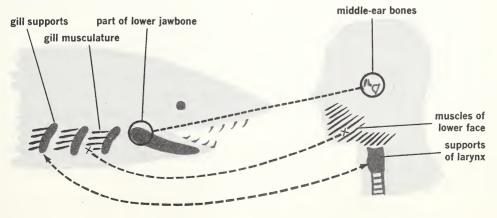
Thus evolution can only remodel and build on what already exists, in small, successive steps. Since, given a long enough time span, every feature of every organism undergoes random variations in many different directions, opportunities for diverse

evolutionary changes have been, and still are, very numerous. Some of these opportunities have been and are actually exploited.

Therefore, every organism, man not excepted, is a patchwork of good opportunities seized by selection at the right time. In man, for example, the bones of the middle ear have arisen opportunistically from pieces of earlier vertebrate jawbones. The musculature of the lower face has evolved from the gill muscles of ancestral fish. The voice box has developed from the gill bones of ancient fish (Fig. 23.8). Such instances of evolutionary opportunism are legion. We consequently conclude that specific organisms are not the result of any planned, goaldirected, or predetermined course of creation. Instead, they are the result of a cumulative, opportunistic process of piece-by-piece building, based on preexisting organisms and governed entirely by natural selection acting on random variations.

This outlines the general nature of the evolutionary process. We have found that, in the past, evolution has proceeded at various rates through

FIG. 23.8. Evolutionary opportunism. The diagram illustrates that evolutionary origin among ancestral fishes of one of the mammalian middle-ear bones, the muscles of the lower face, and the laryngeal cartilages.



successive adaptive radiations; has led to extinction here and to replacement there, to further divergence in some instances, to convergence in others, and to opportunistic exploitation of possibilities in all. As an overall result, the living mass on earth has been increasing fairly steadily in individual numbers and types and has seeped into practically all possible environments. Indeed, it has created new environments in the process. For example, the evolution of trees has created new possibilities of life in the treetops, exploited later by some new plants and by very many new animals, including our own ancestors. The evolution of warm-blooded birds and

mammals has created a new environment in the blood of these animals, exploited later by many new parasites. The evolution of man has created numerous new environments in human installations, and these have been exploited by a large variety of new plants and animals.

We recognize here yet another general characteristic of evolution: a progressive, creative expansiveness, as regards both living mass and ways of life. The expansion is still under way, faster in some cases than in others, and the end cannot be predicted as yet.

REVIEW QUESTIONS

- 1. Describe the essential points of the evolutionary theories of (a) Lamarck, (b) Darwin and Wallace. How could the evolution of giraffes from short-necked ancestors be explained in terms of each of these two theories? What were the weaknesses of each theory?
- 2. Define the modern meaning of natural selection. Show how natural selection has little to do with "survival of the fittest," or "struggle," or "weeding out" and how it is both a peaceful and a creative force. How does it happen that natural selection is oriented toward improved adaptation?
- 3. State the Hardy-Weinberg law. If a Hardy-Weinberg equilibrium exists in a population, what are the rate and amount of evolution?
- 4. What three conditions disturb Hardy-Weinberg equilibria? For each condition, show in what way such equilibria are disturbed and how evolution is therefore affected. How do recessive genes spread through a population? What is genetic drift, and where is it encountered?
- 5. Define "species" in genetic terms. Describe the process of speciation. What are some common geographical isolating conditions, and what is their effect on gene pools? How do reproductive barriers arise between populations?

- 6. Review some actual evidence for evolution. How have rates of evolution varied in the past? What is an adaptive radiation? Illustrate in the case of mammals.
- 7. How many, and which, implications are wholly erroneous in the following statement: "If we examine the evolutionary scale, we find that the lowly ameba has given rise to higher forms such as man." Rephrase this statement into an appropriate number of correct ones.
- 8. What are the general causes of extinction? What has been the pattern of extinction on different taxonomic levels? What is evolutionary replacement? Distinguish between evolutionary divergence and convergence, and give examples.
- 9. In what important way is evolution randomly opportunistic? List 10 structural and functional features of man, and show for each (a) how it has evolved opportunistically, and (b) that it cannot be labeled as being "theoretically best."
- 10. What has been the general evolutionary trend regarding the total quantity of life on earth? Show how evolution has created new environments, hence new opportunities for evolution.

445

SUGGESTED COLLATERAL READINGS

- Blum, H.: Perspectives in Evolution, Am. Scientist, vol. 43, 1955.
- Deevey, E. S.: The End of the Moas, Sci. American, vol. 190, 1954.
- Dobzhanski, T.: The Genetic Basis of Evolution, Sci. American, vol. 182, 1950.
- Dunn, L. C.: Genetic Monsters, Sci. American, vol. 182, 1950.
- Lack, D.: Darwin's Finches, Sci. American, vol. 188, 1953.
- Metcalf, R. L.: Insects vs. Insecticides, Sci. American, vol. 187, 1952.
- Ryan, F. J.: Evolution Observed, Sci. American, vol. 189, 1953.
- Stebbins, G. L.: Cataclysmic Evolution, Sci. American, vol. 184, 1951.

CHAPTER 24

The course of evolution

One of the main lines of investigation which reveals the time course of past evolution is paleontology, the study of *fossils*. Representing the remains of formerly living plants and animals, fossils provide the most direct evidence of the kinds of organisms in existence at various earlier times. A second main line of investigation is comparative morphology, the study of the structure of *presently* living organisms. Being the products of past plants and animals, modern organisms reflect in their architecture the evolutionary history of their antecedents. In particular, three aspects of structure embody the record of past evolution: molecular

structure, revealed by studies in comparative biochemistry; embryonic structure, revealed through comparative embryology; and adult structure, revealed through comparative anatomy.

Unfortunately, the fossil record does not go back more than 500 million years, a span of time representing only the last quarter or so of living history. Events during the crucial first three-quarters must therefore be inferred indirectly through a study of organisms now living.

The 500-million-year mark serves as a convenient time point for dividing the course of evolution into two parts for discussion.

THE FIRST THREE QUARTERS

Geologic time

Fossils are any long-preserved remains of organisms. They may be skeletons or shells, perhaps recrystallized under heat and pressure and infiltrated with mineral deposits from surrounding rock. They may be footprints later petrified, or the remnants of organisms trapped in arctic ice, amber, quicksand, gravel pits, tar pits, and swamps. Or they may be imprints of carbon black on rock, left when the soft parts of plants or animals vaporized under heat and pressure. Whenever a buried organism, or any part of it, becomes preserved in some way before it decays, it will be a fossil.

Fossils formed in the past are embedded in earth layers of different ages. In a geologically undisturbed section of the earth's crust, the deeper layers are the older layers. Material eroded from highlying land gradually piles up on low land and on the sea bottom. Hence a deep layer today was on the surface in past ages and the earth's surface today will be a deep layer in the future. Fossils embedded in successive layers so provide a time picture of evolution. To be sure, deep-lying fossils are normally not accessible. But on occasion, a canyon-cutting river, an earthquake fracture, or an upbuckling and consequent breaking of the earth's crust may expose a cross section through the rock strata. Moreover, erosion gradually wears away top layers, exposing deeper rock. Geological changes of this sort have been sufficiently abundant to expose layers of all different ages in various parts of the world (Fig. 24.1).

How is the actual age of a rock layer determined? Excellent clocks are built right into the earth's crust: radioactive substances. The disintegration rate of these substances is known accurately, as are the endproducts of disintegration. For example, a given quantity of radium is known to "decay" into lead in a certain span of time. When radium and lead are found together in one mass within a rock,

the whole mass presumably had been radium originally, when the rock was formed. From the relative quantities of radium and lead present today, one can then calculate the time required for that much lead to form. This dates the rock exactly to about 10 per cent of its total age. Fossils themselves often help in fixing the age of a rock layer. If such a layer contains a fossil which, on the basis of other evidence, is known to be of a definite age, then the whole layer, including all other fossils in it, is likely to be of the same general age.

Based on data obtained from radioactive and fossil clocks, geologists have constructed a *geologic timetable* which indicates the age of successive earth layers and so provides a calendar of the earth's past history. This calendar consists of five successive main divisions, so-called eras. The last three of these are subdivided in turn into a number of successive periods. The names of the eras and periods and their approximate durations are indicated in Table 11.

The beginning and terminal dates of the eras and periods have not been chosen arbitrarily, but

TABLE 11. The geologic timetable*

Era Cenozoic ("new life")	Period Quaternary Tertiary	Duration		Beginning date
		75	1 74	1 75
Mesozoic ("middle life")	Cretaceous Jurassic Triassic	130	60 30 40	135 165 205
Paleozoic ("ancient life")	Permian Carboniferous Devonian Silurian Ordovician Cambrian	300	25 50 45 35 65 80	230 280 325 360 425 505
Pre-Cambrian		1,500		2,000
Azoic ("without life")		3,000		5,000

^{*}All numbers refer to millions of years; older ages are toward the bottom of the table, younger ages toward the top.



FIG. 24.1. Rock layers of different ages are often exposed to view, as in this photo. The deeper a layer in the earth's crust, the older it is. (American Museum of Natural History.)

have been made to coincide with major geological events known to have occurred at those times. The transitions between eras in particular were times of great upheaval, characterized by mountain building and by severely fluctuating climates. For example, the transition from the Paleozoic to the Mesozoic dates the Appalachian revolution, during which the mountain range of that name was built up. By now, these mountains are already greatly reduced by erosion. Similarly, the transition between the Mesozoic and the Cenozoic was marked by the Laramide revolution, which produced the high mountain ranges of today: the Himalayas, the Rockies, the Andes, and the Alps. As we shall see, these major geological events led to major biological ones, marked by evolutionary crises and largescale replacement of types.

The pre-Cambrian era

The first geologic era, the immensely long Azoic, spans the period from the origin of the earth to the origin of life. Living history begins with the next era, the pre-Cambrian.

Fossils are not lacking altogether from these distant pre-Cambrian ages. But the record is exceedingly fragmentary, and it shows mainly that life, simple cellular life at least, already existed about I

billion years ago. This must mean that the actual origin of life must have occurred earlier, and we place it at about 2 billion years ago, at the start of the pre-Cambrian. We also know how far evolution must have proceeded by the end of the pre-Cambrian, for from that time on we have a continuous and abundant fossil record.

It is a very curious circumstance that rocks older than about 500 million years are so barren of fossils whereas rocks younger than that are comparatively rich in them. Many hypotheses have been proposed to account for this, but to date a satisfactory explanation has not been found. Did the pre-Cambrian environment somehow preclude the formation of fossils? Were fossils destroyed in some way before the Paleozoic? Or is the pre-Cambrian fossil record so scanty because the organisms then were still too unsubstantial to leave fossilizable remains? We simply cannot be sure.

But we *are* reasonably sure that pre-Cambrian evolution must have brought about not only the origin of life and the origin of cells, but also the origin of three of the four present main groups of organisms, the Monera, the Protista, and the Metazoa. Moreover, practically all phyla within these three groups were in existence by the end of the pre-Cambrian. To be sure, the organisms then

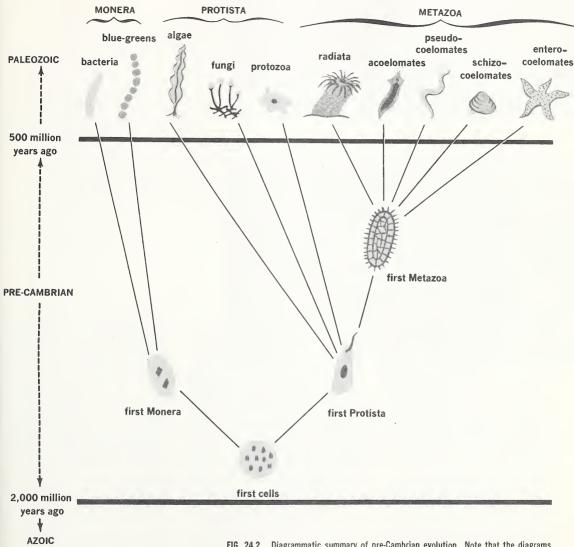


FIG. 24.2. Diagrammatic summary of pre-Cambrian evolution. Note that the diagrams of organisms here used serve only to identify the general groups; they are not intended to indicate actual fossil organisms of 500 million years ago. Indeed, the diagrams suggest modern organisms rather than ancient ones.





FIG. 24.3. Seascapes of the early Paleozoic. Restorations. (a) Cambrian seas. Various algae, trilobites (in center foreground), eurypterids (in center background), sponges, jellyfish, brachiopods, and different types of worms are the most prominent organisms shown. (b) Ordovician seas. The large animal in foreground is a straight-shelled nautiloid. [(a) American Museum of Natural History; (b) Chicago Natural History Museum.]

representing these phyla were not the organisms of today; extinction and replacement by new types was still to occur many times. But the ancient types nevertheless belonged to the same phyla we recognize today.

In what sequence these groups and phyla evolved from the first cells must, in the absence of fossils, be inferred from the nature of presently living organisms. In different contexts, we actually have already made such inferences in various earlier chapters. Thus primitive ancestral cell types are believed to have given rise to two major descendant lines, the Monera and the Protista. Ancestral forms

of these in turn each evolved several subgroups, and so among the early Protista there appeared the algae, the protozoa, and the fungi. These subsequently produced adaptive radiations of their own, leading to the various protistan phyla we know today. Out of one or more of these adaptive radiations also came a new group, namely, the Metazoa. These ancestral animals sooner or later gave rise to five superphyla, viz., the Radiata, the Acoelomata, the Pseudocoelomata, the Schizocoelomata, and the Enterocoelomata. And primitive representatives of these finally produced ancient organisms which typified the various animal phyla of today and which

we now find as fossils dating back some 500 million years (Fig. 24.2).

Note that this presumed sequence of pre-Cambrian events is based on an analysis of actual structures and functions among current organisms, and so probably incorporates a measure of validity as well as a measure of error. The degree of validity is certain to be improved and to be made more detailed through research, but a given degree of error may never be resolved, for direct evidence is simply unobtainable. Note also that the sequence has the form of a bush and consists of a succession of adaptive radiations. This is as it should be, on the basis of known evolutionary mechanisms.

Thus the long pre-Cambrian undoubtedly spanned not only three quarters of evolutionary time, but also three quarters of evolutionary substance. The organisms in existence at the end of the pre-Cambrian probably were all aquatic, and the land apparently had not been invaded as yet. The

ensuing last quarter of evolution brought about principally a rich and extensive further diversification within the existing phyla. This produced replacement of ancient forms by new ones, including in each of the three main groups the evolution of types which could live on land. And among the land-adapted descendants of the Protista, more specifically the green algae, there were types which established a new main group, viz., the Metaphyta.

THE LAST QUARTER

Starting with the Cambrian period of the Paleozoic era, the course of evolution is documented fairly amply by fossils. These show that, on the phylum level, every group in existence in the Cambrian has persisted to the present and, on the species level, no group has persisted. So far as is known, only a single *genus* has survived from the Ordovician, the period after the Cambrian. This

FIG. 24.4. (a) Fossils of trilobites. (b) A eurypterid. (c) A crinoid or sea lily, a sessile echinoderm. (American Museum of Natural History.)







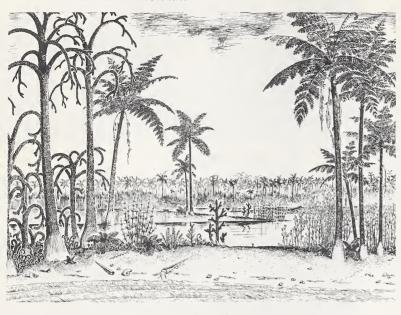


FIG. 24.5. Devonian land plants. Note fern trees, as on right. Psilopsids are shown in middle foreground, along shore, as are sphenopsids, toward left and behind small ferns. The large trees on extreme left are lycopsids. (American Museum of Natural History.)

genus is *Lingula*, of the phylum Brachiopoda (Chap. 9). Apart from this 400-million-year-old relic, all ancient genera have become extinct, like all ancient species. This points up the dominant theme of the fossil record as a whole: very extensive and repeated replacement within major groups and relatively few additions of new major groups.

The Paleozoic

Cambrian and Ordovician. During these two periods, the land surface was as yet free of living organisms, with the possible exception of bacteria. But the sea abounded with diverse types of algae, and among animal groups, sponges, coelenterates, brachiopods, bryozoa (ectoprocts), echinoderms, mollusks, arthropods, and a large variety of worms were particularly common (Fig. 24.3).

The most prominent arthropods were the now extinct eurypterids, large animals resembling crustacea to some extent, but more nearly related to horseshoe crabs and scorpions, and the similarly extinct trilobites, whose bodies were marked into three lobes by two longitudinal furrows. Among mollusks, archaic clams and snails were present, as were the nautiloids (Figs. 24.3 and 24.4). Related to modern squids, octopuses, and particularly to the living chambered nautilus, the nautiloids probably included the largest animals of the time: some had uncoiled shells 5 to 6 yd long.

From the human standpoint, the most important event of the early Paleozoic was the rise of the subphylum Vertebrata. The chordate ancestors of vertebrates probably were marine tunicates, already present at the start of the Paleozoic. Some of the descendants of these ancestral tunicates later evolved into vertebrates, very probably in fresh water. The first fossil vertebrates date to the late Ordovician. These were members of the class Agnatha, the jawless fishes. Lampreys and hagfishes are the only surviving descendants of these forms (Chap. 9).

Silurian and Devonian. The first invasions of the land occurred during the Silurian. Metaphytes, newly evolving at the time from green algal stocks, probably led the move. For in the middle Silurian, the first members of the phylum Tracheophyta appear in the fossil record. These archaic representatives of modern land plants belonged to the subphylum of psilopsids, now virtually extinct (Chap. 8).

Once they had reached the land, the early psilopsids rapidly made the most of the new opportunities. They gave rise to three other major tracheophyte lines, the lycopsids, the sphenopsids, and the pteropsids. The first two of these three new subphyla have since become almost extinct, being represented today only by the *club mosses* and the *horsetails*, respectively. But the third new subphylum, the pteropsid stock, flourished ever since it arose. The earliest representatives of the pteropsids were the ferns, which became well established by Devonian times. Some of these ancestral ferns grew to tree size, and they formed the first forests (Fig. 24.5).

Animals followed the plants to land. Fossil scorpions from the late Silurian are the earliest known terrestrial animals, and other land arthropods appeared in the Devonian: spiderlike creatures, archaic mites, and probably the ancestors of insects. Moreover, at the very end of the Devonian, the first terrestrial vertebrates evolved from fishes.

The Devonian as a whole is often called the age of fishes. During the early Silurian, ancestral jawless fishes had given rise to a new line, the *jawed*

FIG. 24.6. Drawing of a placoderm. (Chicago Natural History Museum.)





FIG. 24.7. Restoration of fossil lobe-finned fishes. (American Museum of Natural History.)

fishes, or placoderms. The name of this separate class of vertebrates refers to the armor plates with which the skins of these fishes were equipped (Fig. 24.6). Placoderms became abundant when the Devonian began, and most exploited the possession of jaws by adopting a fiercely carnivorous way of life. But their dominance was relatively short-lived. For early during the Devonian, ancestral placoderms had given rise to two new lines of fishes, and these came to replace the later placoderms. By the end of the Devonian, placoderms had disappeared completely, the only vertebrate class which has become

The two new types of fishes evolved from early placoderms during the Devonian were the cartilage



FIG. 24.8. The wing of a Permian insect, shown in actual natural size. Insects larger than this existed in the Permian, but even the owner of the wing shown was far larger than any insect today. (Courtesy of Dr. C. O. Dunbar and Peabody Museum, Yale University.)

fishes and the bony fishes, each representing a separate class. The former became largely marine and gave rise to the sharks, skates, and rays.

Bony fishes soon radiated into several subgroups, and one of these, the lobe-finned fishes, included the ancestors of the amphibia, the first land vertebrates. As indicated by their name, the lobe-fins (Fig. 24.7) had fleshy appendages, usable to some extent as walking legs. These fishes probably lived in fresh waters which dried out periodically, and their fins may have enabled them to crawl overland to other bodies of water. Hence terrestrial vertebrates probably arose, not because certain fish preferred the land, but because they had to use the land if they were to survive as fish.

Thus, when the Devonian came to a close, sharks dominated in the ocean and bony fishes in fresh water. On land, forest-forming ferns and other tracheophytic plants were well established, terrestrial arthropods had become abundant, and the first amphibia had made their appearance.

Carboniferous and Permian. In these later Paleozoic times, the character of aquatic life did not change in any major ways but that of terrestrial life did.

The first fossil plants of the phylum Bryophyta date to the Carboniferous. The original ancestors of this phylum in all probability were green algae. Also during this period, many of the forest-forming ferns and other tracheophytes living in swamp regions were buried and became fossilized. Extensive coal beds arose in this manner, among them those in Pennsylvania and West Virginia, for which the period is named.

Undoubtedly the most important event in the plant kingdom was the rise of the seed plants, late during the Carboniferous. These plants evolved from the same pteropsid stock which earlier had given rise to the ferns. The first representatives of the seed plants were cone-bearing types: ginkgoes and cycads, largely extinct today, and several other groups that have now completely disappeared.

Modern conifers too arose from these early seedforming, cone-bearing pteropsids.

In the animal kingdom, some additional terrestrial groups evolved from aquatic ancestors, and some other groups, already terrestrial, began to diversify. More specifically, land snails appeared for the first time during the Carboniferous, centipedes arose, and spiders and scorpions became still more abundant than before. Above all, insects produced extensive adaptive radiations at that time. Some of these ancient insect types reached sizes well above the modern maximum. A Permian dragonfly, for example, is known to have had a wingspread of close to a yard (Fig. 24.8).

Among vertebrates, the amphibia gave rise to a large variety of more or less clumsy, often bizarre forms, the labyrinthodonts (Fig. 24.9). During the Permian, most of these began to be replaced by members of a new vertebrate class, the reptiles. The latter had evolved from ancestral labyrinthodonts late during the Carboniferous. They were represented at first by one main group, the cotylosaurs,

or *stem reptiles*. Inasmuch as they laid hard-shelled land eggs, they were the first completely terrestrial vertebrates. The cotylosaurs produced a major reptilian radiation during the Permian, and so they set the stage for an "age of reptiles," which followed during the Mesozoic era.

Paleozoic history as a whole is summarized in Fig. 24.10.

The Mesozoic and Cenozoic

Apart from reptilian evolution, the Mesozoic era was characterized by several other major events.

During the late Triassic or early Jurassic, the flowering plants arose, probably from cone-bearing pteropsid ancestors. In the Cretaceous, the flowering plants underwent an expansion which established them as the dominant terrestrial plant types from then on. Parallel with this, insects reradiated enormously, and their present importance traces to this Mesozoic expansion. An equally extensive radiation occurred among the bony fishes, and the resulting modern bony fishes became the dominant animals

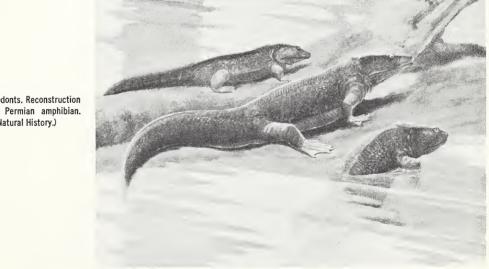
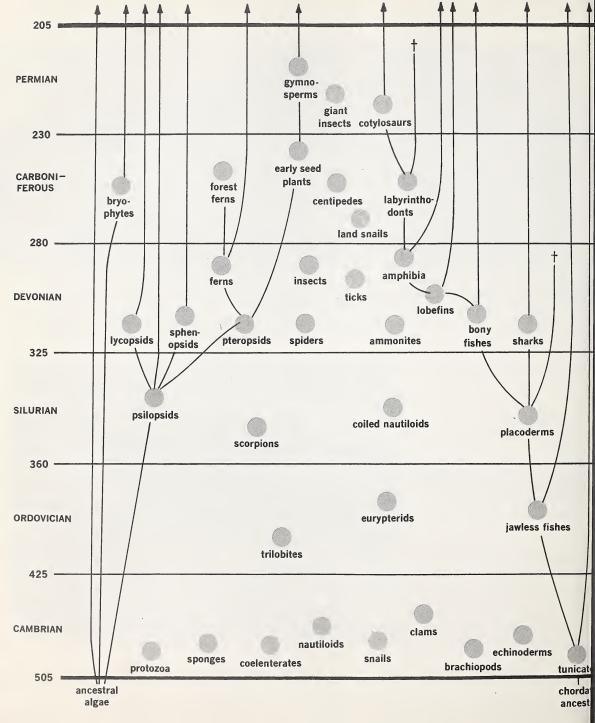


FIG. 24.9. Labyrinthodonts. Reconstruction of Diplovertebron, a Permian amphibian. (American Museum of Natural History.)



of the marine and fresh-water environments, a status they still retain today. Thus both the sea and the land began to acquire a relatively modern character (Fig. 24.11).

However, the most spectacular Mesozoic event was the expansion of the reptiles. These animals not only evolved many different terrestrial ways of life, but also invaded the water and the air. As a group they reigned supreme on earth for 130 million years, longer than any other animals to date. When their dominance was eventually broken, they were replaced by two new groups they themselves had given rise to, the birds and the mammals.

Reptiles. At the beginning of the Mesozoic, five major reptilian stocks were in existence, all evolved during the Permian from the cotylosaurian stem reptiles (Fig. 24.12). One stock, the so-called thecodonts, reradiated extensively during the Triassic and in turn gave rise to the following types: the ancestral birds; the ancestors of the modern crocodiles, lizards, and snakes; the flying pterosaurs; and two other groups, referred to collectively as dinosaurs. A second reptilian stock was ancestral to the modern turtles. A third and fourth produced two kinds of marine reptiles, the porpoiselike ichthyosaurs and the unique, long-necked plesiosaurs. The fifth stock comprised the so-called therapsids, mammal-like reptiles which included the ancestors of the true mammals.

These various reptilian types did not all flourish at the same time. The Triassic was dominated largely by the ancestral thecodonts and the therapsids. The former were rather birdlike in appearance. They featured large hind limbs for walking, an enormous supporting tail, and diminutive fore-

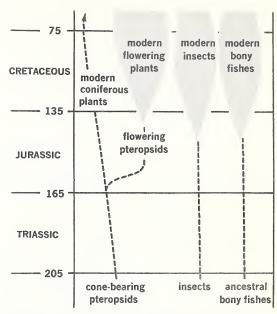


FIG. 24.11. The major nonreptilian radiations of the Mesozoic.

limbs, often not even long enough to shovel food into the mouth. Therapsids, on the other hand, walked on all fours, and some of them gradually became less reptilelike and more mammal-like (Fig. 24.13). True mammals arose from this group during the late Triassic or early Jurassic. However, these new fur-bearing vertebrates were still greatly overshadowed by the reptiles, and they remained small and inconspicuous during the rest of the Mesozoic, that is, for a period of about 80 or 90 million years.

During the Jurassic, ichthyosaurs became abundant in the ocean and one of the thecodont groups evolved into birds. This transition is documented beautifully by a famous fossil animal called *Archaeopteryx* (Fig. 24.14). The organism possessed teeth and a lizardlike tail, two features which are distinctly reptilian. But it also possessed feathers and wings, and presumably it flew like a bird. Like the

i. 24.10. Summary of evolution during the Paleozoic. Read from bottom The level at which a given group is drawn corresponds roughly with the ie of its first appearance in the fossil record. Patterns of descent are win only for the Metaphyta (left part of diagram) and the Chordata (right to of diagram). Of the other groups shown, the trilobites, eurypterids, and monites became extinct by the end of the Paleozoic; all remaining ones resisted, though replacement within each group occurred extensively.

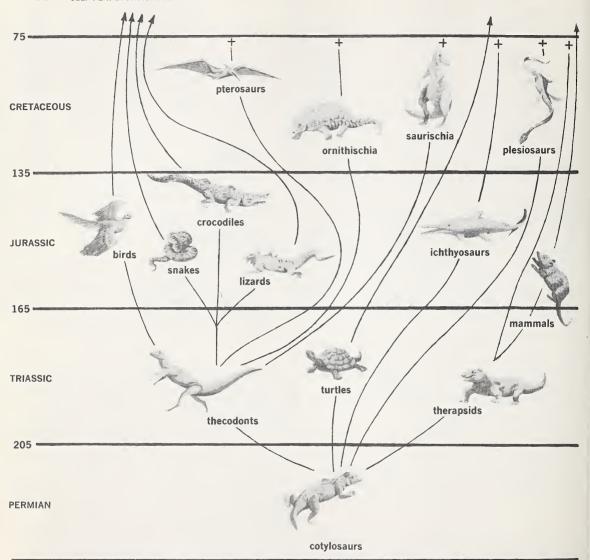


FIG. 24.12. The great reptilian radiation of the Mesozoic. Placement of groups corresponds roughly with the time of their greatest abundance.



FIG. 24.13. Therapsids, mammal-like reptiles of the Triassic. (American Museum of Natural History.)

early mammals, ancestral birds too were inconspicuous during the whole remaining Mesozoic. They were overshadowed particularly by their thecodont kin, the pterosaurs. These flying reptiles had their heyday during the Cretaceous, the period when reptiles as a whole attained their greatest abundance and variety. Plesiosaurs then were common in the ocean, and the dinosaurs came into undisputed dominance on land (Fig. 24.15).

The two dinosaurian groups are called the Ornithischia and the Saurischia. Both evolved from the thecodonts. Not all dinosaurs were large, but some of the group were enormous. The saurischian Brontosaurus was the largest land animal of all time, exceeded in size only by the modern blue whale. This dinosaur was herbivorous, and it probably lived in swamps or lagoons, where it could support its 20- to 30-ton bulk in water. Another saurischian, the giant Tyrannosaurus, probably was the fiercest land carnivore of all time. Among its victims undoubtedly were animals like Ankylosaurus and Triceratops, herbivorous and heavily armored ornithischian giants.

As the Cretaceous came to a close, virtually all the reptilian multitude became extinct. Today the class is represented mainly by turtles, crocodiles, lizards, and snakes. The specific reasons for this large-scale dying out have been sought for a long time, but fully satisfactory explanations have not yet been found. Climatic changes at the end of the Mesozoic, coincident with the Laramide revolution, are believed to have played a decisive role. Mesozoic reptiles were adapted to rather warm environments, as their modern descendants still are. However, climates appear to have become colder toward the close of the Cretaceous, as a result of the Laramide revolution. Much tropical and subtropical vegeta-

FIG. 24.14. Cast of Archeopteryx. Note feathered tail, wings. Head is bent back, and teeth-bearing mouth is not easily visible here. (American Museum of Natural History.)



tion then must have died out, which must have meant that herbivorous reptiles lost their food supplies. And as the herbivorous stocks so declined, the carnivorous reptiles would have had to die out too.

Whatever the precise causes, the extinction of the Mesozoic reptiles cleared the way for a great expansion of mammals and birds.

Mammals. The radiation of mammals and birds came to be the key feature of the new Cenozoic era. Terrestrial mammals replaced the dinosaurs; aquatic mammals eventually took the place of the former ichthyosaurs and plesiosaurs; and bats, but more especially birds, gained the air left free by the pterosaurs. The Cenozoic is often designated as the "age of mammals," but it might equally well be called the "age of birds."

At the beginning of the 75-million-year-long Cenozoic, ancestral mammals gave rise to a large-scale radiation of some two dozen independent lines. Some of these became extinct, but most persist today. They represent three subclasses and some twenty orders within the class of mammals (Fig. 24.16, also Chap. 9). The subclass *Eutheria*, or placental mammals, are the most abundant group. To it belong the most familiar mammals: cats, dogs, seals, and walruses; rodents; whales and dolphins; bats; moles and shrews; cattle, sheep, pigs, and camels; horses and zebras; elephants and tapirs; monkeys and man; and many others.

In the following discussion, we shall concentrate primarily on the history of one of the mammalian groups, namely, the line of mammals which produced man.

THE EVOLUTION OF MAN

The primate background

The origin of primates. Just as each geological era may be subdivided into periods, so each period in turn may be subdivided into epochs. The periods and epochs of the Cenozoic era are shown in Table 12. As noted earlier, the era as a whole began

with the great upheavals of the Laramide revolution, which produced the present high mountain ranges. Their emergence substantially changed the pre-Cenozoic patterns of air circulation between ocean and land, and the new patterns led to new climatic conditions. For example, the east-west barrier of the Himalayas in Asia, and of the Alps in Europe, prevented warm south winds from reaching the northern portions of Eurasia. These regions became cooler as a result. In turn, this undoubtedly facilitated the development of ice ages during the recent Pleistocene epoch.

TABLE 12. The epochs and periods of the Cenozoic era*

Period	Epoch	Duration	Beginning date
Quaternary	Recent	20,000 years	20,000 в.с.
	Pleistocene	1	1
Tertiary	Pliocene	11	12
	Miocene	16	28
	Oligocene	11	39
	Eocene	19	58
	Paleocene	17	75

^{*} Unless otherwise stated, all figures refer to millions of years.

Ice ages had occurred before during the earth's history, and during the last million years there were four. In each, ice sheets spread from the North Pole southward, covered much of the land of the Northern Hemisphere, then receded. Warm interglacial periods intervened between successive ages of glaciations.

The last recession began some 20,000 years ago, at the beginning of the Recent epoch, and it is still in progress: polar regions are still covered with ice. The biological importance of Cenozoic climates in general, and of Pleistocene ice in particular, is great, for these environmental conditions materially influenced the evolution of all mammals, man not excepted. Man in a sense is one of the products of the ice ages.

When the Cenozoic began, the great mammalian



FIG. 24.15. Reconstruction of plesiosaurs (left) and ichthyosaurs (right). (Chicago Natural History Museum.)

FIG. 24.16. Some of the main features of the mammalian radiation during the Cenozoic.

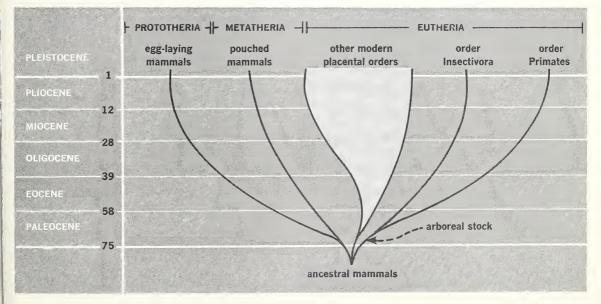




FIG. 24.17. Arboreal squirrel shrew. This animal belongs to the order Insectivora. (American Museum of Natural History.)

radiation was just getting under way (Fig. 24.16). Each descendant mammalian line exploited a particular way of life available at the time and came to occupy either a new environmental niche or one left free after the extinction of the Mesozoic reptiles. One mammalian line is of particular interest, for it eventually led to man. This line exploited a relatively new environmental possibility. Its members took to the trees, then already abundantly available, and adapted to an *arboreal* life.

Soon after such a stock of arboreal mammals had evolved during the early Paleocene, it must have reradiated and produced two major sublines, the order *Insectivora* and the order *Primates* (Fig. 24.16). Most modern insect-eating mammals, particularly the moles and the hedgehogs, are clearly distinct from modern primates, of which man is a late member. But some of the shrews now living are exceedingly like insectivores on the one hand and like primitive living primates on the other. Indeed, one group of shrews is actually classified with the Insectivora, and another with the Primates. Fossil data too support the view that insectivorous mammals and primates are very closely related, through a common, shrewlike, arboreal, insecteating ancestor (Fig. 24.17).

The primate radiation. The first distinct primates evolved from this insect-eating ancestor during the Paleocene are known as the early prosimians. They were small, still shrewlike in appearance, with a fairly long snout and a long bushy tail. They were also agile and nimble, an important adaptation in a life among the treetops. Undoubtedly they possessed good eyes and good neuromuscular coordination, but in these respects they were probably not equipped very much better than early mammals in general. Of the many lines which radiated from the early prosimians during the Paleocene, four major ones survive today (Fig. 24.18).

One of these four largely retained the prosimian characteristics and gave rise to a number of sublines during subsequent epochs. The modern prosimians are the collective result. This group includes the lemurs and the aye-ayes, found today largely on the island of Madagascar (Fig. 24.19). These animals still possess long snouts and long tails, but instead of claws they possess flat nails, a general primate characteristic. Nails probably interfere less with locomotion along tree branches than long claws; hence nails may be a specific adaptation to arboreal life. The modern prosimians also include the tarsiers of southern Asia and Indonesia (Fig. 24.19). In these, the snout has receded considerably and a fairly well-defined face has appeared. Moreover, the eyes, which in lemurs are still more or less on the

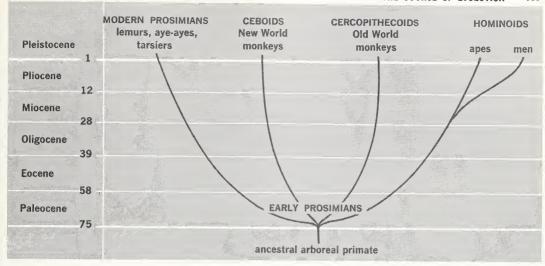


FIG. 24.18. Diagram of the radiation of primates.

side, have moved well into the face. As a result, tarsiers are able to focus on one point with both eyes, and this endows them with stereoscopic vision and efficient depth perception.

These features are additional adaptations to a tree-dwelling existence. In a plains animal such as a horse, for example, the eyes are located advantageously on the side, where they enable the animal to scout the open environment even while grazing. But among the branches of a tree lateral vision is less important. Quite the contrary, it becomes important to look ahead along a branch, almost a necessary requirement if balance is to be retained during precarious limb-over-limb locomotion. Note too that tarsiers possess fairly well defined fingers, with a gripping pad at the end of each.

The second of the main groups descended from the early prosimians comprises the ceboids, or *New World monkeys*. These attained their present diversity during the Oligocene and Miocene. Ceboid monkeys today are confined to South and Central America, and they are characterized by long strong tails, which are used as fifth limbs. The third main group evolved independently from Paleocene prosimians consists of cercopithecoids, or *Old World monkeys*. They too radiated during the Oligocene and Miocene, and they are found today in Africa and Asia. These monkeys possess tails, but they are not used as limbs.

In both groups of monkeys, adaptations to arboreal life have evolved a good deal further than in modern prosimians. A monkey possesses a very well developed face, stereoscopic vision, and in addition independently movable fingers on all four limbs. Moreover, it possesses opposable thumbs, which allow it to grip tree branches very firmly. Also, limbs may be rotated freely within their sockets. In a plains animal like a horse, limbs move predominantly back and forth. The limb sockets here permit very little lateral play, and this is an energy-saving feature in running. In jumping among tree branches, on the other hand, freely movable limbs are clearly advantageous.

Correlated with such skeletal specializations to





FIG. 24.19. (a) A modern lemur from Madagascar. (b) A modern tarsier from Indonesia. (American Museum of Natural History.)

arboreal life, monkeys have also evolved important muscular, sensory, and neural adaptations. Through a general enlargement of the cerebral cortex and a particular enlargement of the optic lobes, monkeys have become capable of precision timing, of judging distances to the inch, and of coordinating limb and finger muscles in new, complex ways. In turn, increase in brain size has led to a quickness of mind and a level of intelligence well above the prosimian average. We may note here that the evolution of intelligence has been correlated particularly with

the improvement of coordination between the eyes and the limbs. Evidently, primate intelligence too is basically an adaptation to the arboreal way of life.

The hominoid radiation. Trends of the same kind, but developed very much further than in monkeys, are apparent also in the fourth group of living primates. Descended independently from Paleocene prosimians, this group comprises the so-called hominoids. During the early Miocene, some 30 million years ago, the hominoid line radiated into two main sublines. One of these led to the apes, the other to man (Fig. 24.18). Both groups are characterized by the absence of an external tail and by an increase in body size over the average of other primates. Moreover, they feature a still further, very remarkable enlargement and elaboration of the brain.

Apes are represented today by four genera: gibbons, orangutans, chimpanzees, and gorillas. The group is fundamentally arboreal, and the ancestral hominoid stock undoubtedly was too. But modern apes include types which have abandoned the arboreal way of life more or less completely. Orangutans, for example, and especially chimpanzees, can be quite at home out of trees. And gorillas are ground animals altogether, using trees as little as man. Correlated with this abandonment of life in trees is a tendency toward more or less two-legged walking and toward a more or less upright posture. In this, arboreal adaptations can be used to advantage. For example, the long arms of a gorilla enable it to assume a half-erect, crouching stance, and the animal may also support itself on its hind legs and walk bipedally for short distances. This frees the agile forelegs and fingers for other tasks.

These trends became very much more elaborated in the line leading to man. After branching away from the common hominoid stock during the Miocene, the human line left the trees completely. Forelimbs remained adapted for gripping, but the feet evolved into flat walking platforms. A halferect, bent-kneed, four-limbed shuffle must have been characteristic for a long time, but as the feet

became perfected, forelimbs were completely relieved of a locomotor function. Undoubtedly, it was this total freeing of arms and fingers for many new functions that made possible the evolution of the most basic human characteristics. For, correlated with new opportunities for exceedingly complex hand-eye coordination, brain size enlarged still further and intelligence increased spectacularly.

These and other features which now distinguish man and apes came to be superimposed on the characteristics of pre-Miocene arboreal primates. We recognize, therefore, that the modern human type could not have evolved if the ancestral type had not first been specialized for life in trees.

The prehuman line

Early history. Leaving the trees was clearly essential to the emergence of man. What prompted our Miocene ancestors, and also some of the early apes, to abandon arboreal life? A certain answer is not available, but a reasonable guess may be made: in the ancestral territories, trees may have become scarce.

A thinning out of deciduous forests may have been generally characteristic of the late Tertiary, as a result of steadily cooling climates. Small annual plants and evergreens would be favored under such conditions, but dense accumulations of perennial deciduous trees would become confined largely to tropical regions. Elsewhere, such trees would become sparser, and continuous overhead canopies of branches and foliage would therefore disappear. Hence our prehuman ancestors would have had to travel on the ground if they wished to move from one stand of trees to another. However, such forced excursions may well have been fraught with considerable danger. For saber-toothed carnivores and other large mammals dominated the ground at those times. Consequently, ability to dash quickly across open spaces may have had great selective value, and this may have oriented the evolution of running feet in the human direction. Moreover, strong muscles would be required to move the hind

limbs in new ways. Indeed, a unique trait of the human line is the possession of such muscles, in the form of enlarged buttocks.

It is conceivable, therefore, that the prehumans came out of the trees because they had to, and that this in turn promoted the gradual evolution of running feet, bipedal locomotion, newly functioning forelimbs, complex hand-eye coordination, and powerful brains.

We may note here that the early evolutionary history of the human line must necessarily be speculative, for fossil data of Miocene and Pliocene prehumans are almost completely lacking. Indeed, the whole human fossil record is tantalizingly scanty, and we can trace the recent evolution of almost any other mammal far better than our own. Virtually the entire fossil evidence of human evolution is of Pleistocene origin, that is, no older than 1 million years. However, this epoch does include the development of modern man, and some fossil documentation of this event is available.

Dominated by intermittent ice ages, the Pleistocene as a whole was a period of severe and fluctuating climates. It was marked by extinction of many forms and by rapid evolution of others. Adaptation to cold was of prime importance. Many mammals and other forms migrated south beyond the reaches of ice, and their descendants are found today among the animal populations of equatorial and subequatorial regions. Others, like the woolly mammoth, possessed rich fur and could hang on for a time in the cold lands. Still others withdrew into caves, forests, and ground holes and managed to eke out a precarious existence. But they survived, and today bears, moose, and many small mammals still live in northern regions. Among the cave dwellers may have been a number of subhuman types, descended from Tertiary prehuman ancestors. As noted, it is not known what the specific ancestors of these subhumans may have been. Nor is it known which of the subhumans finally gave rise to modern man. Nevertheless, fossils of Pleistocene subhumans provide a good indication of how far the human line had evolved since Miocene times.

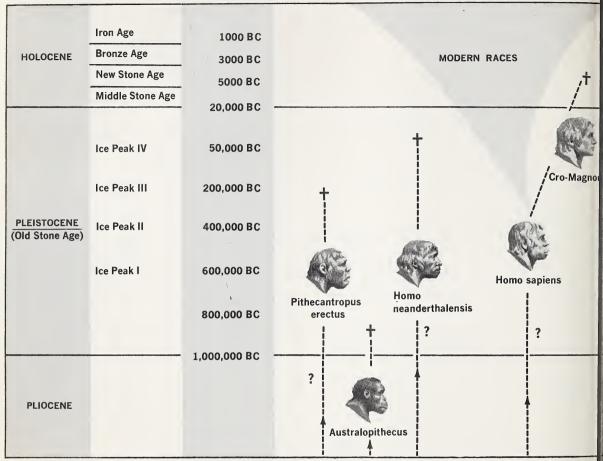


FIG. 24.20. The Pleistocene and man. Each humanoid type is shown at a time level at which that type is actually known to have existed. It is not clearly established when a given type first originated, nor when exactly it became extinct.

Pleistocene subhumans. It is not necessary to find whole fossilized skeletons to reconstruct the probable appearance of their once living owners. The proportions of body parts to one another may be deduced with reasonable accuracy from living man, from apes, and from such whole skeletons of sub-

human types as have been found. For example, a tooth, a jawbone, a skullcap, or a leg bone may not only be identified from its shape as belonging to a particular subhuman, but may also give important clues about the missing remainder. By and large, the features of the skull tell most. Thick or thin

bones, prominent or reduced eyebrow ridges, receding or vertical forehead, small or large brain case, poorly or well-defined chin, all indicate fairly well whether or not a fossil is from a primitive or an advanced subhuman type. Much may also be learned from various signs of cultural activity often associated with a fossil find. For example, the type of tool, the type of camp site, the type of weapon found with a fossil, each may reveal a great deal about the evolutionary status of the subhuman in question.

Some of the known aspects of subhuman history during the last million years or so are outlined in Fig. 24.20. The oldest subhuman fossil found to date has been assigned the generic designation Australopithecus. Rather more apelike than manlike, this humanoid dates to the late Pliocene. It is believed to be fairly closely related to the unknown ancestral stock from which Pleistocene subhumans must have evolved.

Among several known subhumans of the early Pleistocene, one is documented fairly well. This is Pithecanthropus erectus, the Java ape man, dating back perhaps 500,000 years and probably more (Fig. 24.21). Pithecanthropus was already more manlike than apelike. He possessed a brain measuring about 1,000 cm3 by volume, which compares with 600 cm3 for the gorilla and about 1,500 cm3 for the brain of modern man. Pithecanthropus, in addition, featured a flat sloping forehead, thick eyebrow ridges, and a rounded, practically chinless jaw. He had relatively long arms, and he probably crouched like a gorilla. Also, he may have practiced cannibalism: separate skullcaps have been found, detached cleanly from the rest of the skeletons. Sheer accident is not likely to have caused such neat separations.

The best known of the subhumans is undoubtedly *Homo neanderthalensis*, the Neanderthal man (Fig. 24.21). He was sufficiently like modern man to be put into the same genus, *Homo*, but he represented a distinctly different species. The Neanderthalers flourished during the latter half of the Pleistocene, roughly from about 500,000 to 50,000



FIG. 24.21. The presumed appearance of prehistoric men. Reconstruction, based on skull structure. From left to right: Pithecanthropus, Neanderthaler, Cro-Magnon. (American Museum of Natural History.)

years ago. Therefore the first Neanderthalers could have been contemporaries of the last members of the *Pithecanthropus* stock. The Neanderthalers still had practically no chin, still had heavy brow ridges, fairly long arms, short legs, and a crouching gait. But their brain case was deeper and higher, enclosing a volume of about 1,500 cm³. This approximates the brain size of modern man, but the Neanderthal brain was proportioned differently. The skull jutted out in back, where we are relatively rounded, and the forehead was low and receding.

Culturally, the Neanderthalers were Stone Age cave men. All Pleistocene human and subhuman types are generally regarded as belonging to the Old Stone Age (Fig. 24.20). But whereas earlier subhumans made only crude stone implements, Neanderthal men fashioned a variety of weapons, tools, hunting axes and clubs, and household equipment. Yet he was still a nomad living from hand to mouth, and he had neither agriculture nor domesticated animals. He did not make pottery, and he did not leave any art. His territory covered most of Europe, with fringe populations along the African and Asian coast of the Mediterranean (Fig. 24.22).

Neanderthal man, and his contemporary sub-

humans in other parts of the world, held their own until relatively recently, paleontologically speaking. Then they became extinct and were replaced by already existing representatives of our own species, *Homo sapiens*.

Modern man

History. The time of origin of modern man cannot be pinpointed very precisely. The oldest known fossil of Homo sapiens is probably the Swanscombe skull plate, and this skeletal fragment may date back about 300,000 years. At that time, modern man clearly was already in existence. It is possible, therefore, that Homo sapiens may have arisen as long as half a million years ago. His early representatives, like the Neanderthalers, may have been contemporaries of Pithecanthropus.

The specific derivation of modern man is still in question too. Neither *Pithecanthropus* nor Neanderthal man is likely to have been ancestral to us. Instead, *Homo sapiens* and the subhuman types of the Pleistocene appear to be separate branches of a humanoid radiation. The original ancestor of this radiation is not known, and with one exception, namely, ourselves, all other branch lines of the radiation are now extinct.

The modern men who replaced the Neanderthalers in Europe are known as the Cro-Magnon race (Fig. 24.21). This group flourished from about 50,000 to 20,000 years ago, roughly the peak period of the last ice age. Cro-Magnon was fully erect, 6 ft tall on the average, with a brain volume of about 1,700 cm3. His culture still belongs to the Old Stone Age, but in addition to stone implements, Cro-Magnon used bone tools. Bone needles have been found with which he may have sewn animal skins into crude garments. The dog became his companion, but he still did not domesticate food animals, and he did not practice agriculture; Cro-Magnon was a cave-dwelling hunter. He developed a remarkable art, however, as his murals on cave walls indicate.

In other parts of the world there lived other races of *Homo sapiens*. The racial division of modern man into caucasoids, negroids, and mongoloids

may have taken place then. But the original racial traits became diluted or obliterated fairly rapidly, through interbreeding among the extensively migrating human populations. None of the present human types represents a "pure" race.

As the Pleistocene came to a close, Cro-Magnon disappeared in Europe and other groups of modern man replaced him. At that time, some 20,000 years ago, the ice sheets started to retreat, milder climates gradually supervened, and eventually man no longer needed to shelter in caves. For the next 15,000 years he produced what is known as the Middle Stone Age culture. It was characterized chiefly by great improvements in stone tools. Man was still a nomadic hunter.

The New Stone Age began around 5000 B.C., about the time Abraham settled in Canaan. A great cultural revolution took place then. Man learned to fashion pottery; he developed agriculture; and he was able to domesticate animals. From that period on, modern civilization moved on with rapid strides. By 3000 B.C. man had entered the Bronze Age, and during the ensuing 2,000 years, the Iron Age, he was to find out how to produce and to work iron. Not very long after he discovered steam, electricity, and now the atom and outer space. Measured by geological standards, the hairy beast which lumbered down from the trees 30 million years ago turned into college professor in a flash.

The status of man. That modern man has evolved through the operation of the same forces which produced all other organisms is clear. And it should also be clear that this organism is by far the most remarkable product of evolution. Man is sometimes described rather offhandedly as being "just" another animal. Often, on the contrary, he is considered to be so radically distinct that the appellation "animal" assumes the character of an insult. Neither view is justified.

Man certainly is an animal, but an animal with very unique attributes. Structurally, man is fully erect and possesses a double-curved spine, a prominent chin, and walking feet with arches. He is a fairly generalized type in most respects, being not



FIG. 24.22. Restoration of a Neanderthal group. (Chicago Natural History Museum.)

particularly specialized for either speed, strength, agility, or rigidly fixed environments.

At some stage during his evolution, his rate of embryonic development slowed down and his whole life cycle became stretched out in duration. Thus man became perhaps the longest-lived of all animals. This stretching of the life cycle also lengthened substantially the period of postnatal growth and adolescence. In this manner, another uniquely human characteristic emerged, namely, a proportionately very long youth. A chimpanzee, mature at the age of two, is senile at the age of twenty, when man is only beginning to attain adulthood. Man therefore has time to learn and to gather experiences, and in his learning capacity man is also unique. To be sure, other animals may learn too, but the quantitative difference is so great that it is in effect a qualitative difference.

Learning presupposes a powerful brain, and in this department man clearly has no equal. Note here again that the human nervous system develops as it does because it has *time* to do so, because the embryonic period is greatly stretched out. The most characteristically human traits depend directly or indirectly on man's brain. Man is far more aware of himself and far more individualized in personality and behavior than any other creature. He displays a greater range of emotions than any other animal, and he is the only animal able to laugh and to

weep. Moreover, only man knows beauty, and the human capacities of planning ahead, of having reasoned purposes, and of making considered choices far outclass anything similar in the animal kingdom.

Above all, only man has traditions, and only he *accumulates* knowledge over successive generations. The transmission of knowledge occurs by nonbiological means, and we actually deal here with a new kind of evolution. The old is biological evolution, and its vehicle is the gene. The new is social evolution, and its vehicle is spoken and written *speech*. Man is quite unique in having evolved, and in continuing to evolve, through inherited traditions passed on not only by genes but also by *words*.

Conceivably, this change-over from the merely biological to the human may have as much future significance as the earlier change-over, 2 billion years ago, from the inorganic to the biological. The first transition placed matter on a totally new plane, and on this plane it became organized into a wealth of previously nonexistent arrangements. The recent transition may create new possibilities of like scope. But the realization of this potential is now in the hands of man. For with the coming of man, the chance operations of nature have begun to be modified and manipulated by human purpose. The activities of man block chance increasingly, and man's fate will therefore be decided by man's purpose.

REVIEW QUESTIONS

- 1. What is a fossil? How can the age of a fossil be determined? Review the names and dates of the geological eras and periods. What were the Appalachian and Laramide revolutions? List the major groups of organisms not yet in existence 500 million years ago.
- 2. Describe the key events of evolution during the (a) Cambrian-Ordovician, (b) Silurian-Devonian, (c) Carboniferous-Permian. Review the course of vertebrate evolution during the entire Paleozoic.
- 3. Describe the main events of evolution during the Mesozoic and Genozoic. Review the principal features, and the time pattern, of the Mesozoic reptilian radiation. Name reptilian stocks now extinct and stocks now in existence.
- 4. How many, and which, vertebrate classes have evolved since the Cambrian, and which ones survive today? Trace the ancestry of flowering plants since the Cambrian.
- 5. Name the subclasses of mammals. Describe the principal features of the Cenozoic mammalian radiation, with special attention to the origin of primates.
- 6. Describe the major features and the time pattern of the primate radiation, and name living animals representing each of the main lines. When, and from where, did the line leading to man branch off?

- 7. Describe the various adaptations of each of the primate stocks to arboreal life. Which structural, functional, and behavioristic features of man trace back specifically to the arboreal way of life of his ancestors? How does the hominoid line differ from other descendants of early prosimians? How does the human line differ from that of the apes?
- 8. Why did the prehuman line probably cease to be arboreal? What structural and functional developments were made possible by this descent to the ground? Describe the climatic pattern of the Pleistocene. Show how the Pleistocene glaciations may in part have been consequences of the Laramide revolution.
- 9. Describe and contrast the main fossil subhumans. When was each of them probably in existence? What culture was associated with each?
- 10. Roughly when did modern man evolve? Review in detail the biological characteristics which man shares with (a) all other hominoids, (b) all other primates, (c) all other mammals. Review in detail the biological characteristics which distinguish man uniquely from all other animals.

SUGGESTED COLLATERAL READINGS

- Abelson, P. H: Paleobiochemistry, Sci. American, vol. 195, 1956.
- Bogert, C. M.: The Tuatara: Why Is It a Lone Survivor? Sci. Monthly, vol. 76, 1953.
- Broom, R.: The Ape-men, Sci. American, vol. 181, 1949.
 Brues, C. T.: Insects in Amber, Sci. American, vol. 185,
- Colbert, E. H.: The Ancestry of Mammals, Sci. American, vol. 180, 1949.
- Deevey, E. S.: Radiocarbon Dating, Sci. American, vol. 185, 1951.
- Eiseley, L. C.: Antiquity of Modern Man, Sci. American, vol. 179, 1948.

- ----: Fossil Man, Sci. American, vol. 189, 1953.
- ——: Man, the Firemaker, Sci. American, vol. 191, 1954.
- Janssen, R. E.: The Beginnings of Coal, Sci. American, vol. 179, 1948.
- Jarvik, E.: The Oldest Tetrapods and Their Forerunners, Sci. Monthly, vol. 80, 1955.
- Krogman, W. M.: What We Do Not Know about Race, Sci. Monthly, vol. 57, 1943.
- ----: The Man-apes of South Africa, Sci. American, vol. 178, 1948.
- Millot, J.: Coelacanth, Sci. American, vol. 193, 1955.

GLOSSARY¹

- acoel, acoelomate (ā·sēl') [Gr. a, not, + koilos, cavity]:
 (1) without coelom; also a group of free-living flatworms without digestive cavity; (2) an animal without coelom, i.e., flatworms, proboscis worms, and spinyheaded worms.
- acrosome (ăk'rô·sōm) [Gr. akros, outermost, + soma, body]: structure at the tip of the sperm head (nucleus) which makes contact with the egg during fertilization.
- adenine (ăd'ē · nēn): a pyrimidine component of nucleotides and nucleic acids.
- adenosine (di-, tri-) phosphate (ADP, ATP) (â · dĕn'ô · sēn): phosphorylated organic compounds functioning in energy transfers within cells.
- adrenal, adrenalin (ăd · rē'năl, ăd · rēn'ăl · in) [L. ad, to, + renalis, kidney]: (1) endocrine gland; (2) the hormone produced by the adrenal medulla.
- adrenergic (ăd'rĕn · ûr'jīk): applied to nerve fibers which release adrenalinlike substance from their axon terminals when impulses are transmitted across synapses.
- adventitious (ăd'věn · tish'ŭs): appearing not in usual place; as in adventitious root, which may sprout from anywhere on a stem.
- aerobe, aerobic (ā'ĕr · ōb, -ō'bĭk) [Gr. aeros, air, + bios, life]: (1) oxygen-requiring organism; (2) pertaining to oxygen-dependent form of respiration.
- Agnatha (ăg'nā · thā) [Gr. a, not, + gnathos, jaw]: jaw-
- ¹ The system of indicating pronunciation is used by permission of the publishers of Webster's New Collegiate Dictionary. Copyright 1949, 1951, 1953, 1956, 1958 by G. & C. Merriam Co.

- less fishes, a class of vertebrates including lampreys and hagfishes.
- alga (ăl'ga), pl. algae (-jē): any member of a group of ancient plant phyla; blue-green, green, golden-brown, brown, red algae.
- allantois (ǎ·lǎn'tò·is) [Gr. allantoeidēs, sausage-shaped]: one of the extraembryonic membranes in reptiles, birds, and mammals; functions as embryonic urinary bladder or as carrier of blood vessels to and from placenta.
- allele (å·lēl') [Gr. allēlōn, of one another]: one of a group of alternative genes which may occupy a given locus on a chromosome; a dominant and its correlated recessive are allelic genes.
- amino, amino acid, amination (ă · mē'nō, ă · mĭnā'shǔn):

 (1) —NH₂ group; (2) acid-containing amino group, general structure NH₂—R—COOH, constituent of protein; (3) addition of amino group to other compound.
- amitosis (am'i tō'sīs) [Gr. a, not, + mitos, thread]: form of cell division in which mitotic nuclear changes do not occur; the term applies to a large variety of different kinds of cellular reproduction.
- amnion, amniote, amniotic (ăm'ni · ŏn) [Gr. dim. of amnos, lamb]: (1) one of the extraembryonic membranes in reptiles, birds, and mammals, forming a sac around the embryo; (2) any reptile, bird, or mammal, i.e., any animal possessing an amnion during the embryonic state; (3) pertaining to the amnion, as in amniotic fluid.

- Amphineura (ăm'fi · nū'ra) [Gr. amphi, both, + neuron, nerve]: a class of mollusks, including the chitons, characterized by a primitive ladder-type nervous system.
- amylase (ăm'i · lās) [L. amylum, starch]: an enzyme promoting the decomposition of polysaccharides into smaller carbohydrate units.
- anaerobe, anaerobic (ăn · ã'ēr · ŏb, -ō'bĭk) [Gr. an, not, + aeros + bios]: (1) an oxygen-independent organism;
 (2) pertaining to an oxygen-independent form of respiration.
- anaphase (ăn'á · fāz) [Gr. ana, up, + phasis, appearance]: a stage in mitotic cell division, characterized by the migration of chromosome sets toward the spindle poles.
- anatomy (a · năt'ô · mī) [Gr. ana, up, + temnein, to cut]: the gross structure of an organism, or the science which deals with gross structure; a branch of the science of morphology.
- angiosperm (ăn'jī·ô·spûrm') [Gr. angeion, a vessel, + sperma, seed]: a member of a class of tracheophytic plants, characterized by the possession of flowers and fruits; a flowering plant.
- annelid, Annelida (ăn'ē·lǐd) [L. anellus, a ring]: (1) a segmented worm; (2) the phylum of segmented worms. antheridium (ăn'thêr·ĭd'ī·ŭm) [Gr. anthêros, flowery]:

the sperm-producing organ of plants.

- anthocyanin (ăn'thô sĩ'á nǐn) [Gr. anthos, flower, + kyanos, blue]: a water-soluble pigment in plants, producing red, purple, and blue colors.
- antibody (ăn'ti · bŏd'ī): a substance, produced within an organism, which opposes the action of another substance; in specific usage, an antibody is a globulin type of protein which combines and renders harmless an antigen, i.e., a foreign protein introduced into an organism by infectious processes.
- antigen (ăn'tĭ · jĕn): a foreign substance, usually protein in nature, which elicits the formation of specific antibodies within an organism.
- apical (ăp'ī·kăl) [L. apex, tip]: belonging to an apex, being at or near the tip; as in apical meristem, the embryonic plant tissue at the tip or root or stem.
- archegonium (är'kė · gō'nĭ · ŭm) [Gr. archegonos, first of a race]: the egg-producing organ of plants.
- archenteron (är·kĕn'tēr·ŏn) [Gr. archein, to be first, + enteron, gut]: the central cavity of a gastrula, lined by endoderm, representing the future digestive cavity of the adult.
- arthropod, Arthropoda (är'thrö•pŏd, är•thrŏp'ó•dá) [Gr. arthron, joint, + podos, foot]: (1) a jointed-legged

- invertebrate, such as an insect or a crustacean; (2) the phylum of jointed-legged invertebrates.
- ascus (ăs'kŭs) [Gr. askos, a bladder]: the tubular spore sac of a class of fungi; eight spores typically form within an ascus.
- atom (ăt'ŭm) [Gr. atomos, indivisible]: the smallest whole unit of a chemical element, composed of given numbers of protons, neutrons, and other particles which form an atomic nucleus and of given numbers of electrons, which orbit around the nucleus.
- auricle (ô'rī·k'l) [L. dim. of auris, ear]: a chamber of the heart receiving blood from the circulation and pumping it into a ventricle.
- autosome (ô'tō · sōm) [Gr. autos, self, + soma, body]: any chromosome which is not a sex chromosome.
- autotroph, autotrophism (ô'tô · trŏf', -ĭz'm) [Gr. autos, + trophos, feeder]: (1) an organism which manufactures organic nutrients from inorganic raw materials; (2) a form of nutrition in which only inorganic substances are required as raw materials.
- auxin (ôk'sīn) [Gr. auxein, to increase]: one of a group of humoral agents in plants, promoting cell elongation, hence growth.
- axon (ăk'sŏn): an outgrowth of a nerve cell, conducting impulses away from the cell body; a type of nerve fiber.
- bacillus (ba·sĭl'ŭs) [L. dim. of baculum, rod]: any rodshaped bacterium.
- bacteriophage (băk · tēr'ī · o · fāj) [bacterium + Gr. phagein, to eat]: one of a group of viruses which infect, parasitize, and eventually kill bacteria.
- bacterium (băk · tēr'ī · ǔm) [Gr. dim. of baktron, a staff]: a small, typically unicellular organism characterized by the absence of a formed nucleus; genetic material is dispersed in clumps through the cytoplasm.
- basidium (bā·sīd'ī·ŭm) [Gr. dim. of basis, base]: a spore-bearing organ of a class of fungi; typically four spores are formed on each basidium.
- benthos, benthonic (běn'thŏs) [Gr., depth of the sea]:
 (1) collective term for organisms living along the bottoms of oceans and lakes; (2) adjective.
- beriberi (bĕr'ī·bĕr'ī) [Singhalese beri, weakness]: disease produced by deficiency of vitamin B₁ (thiamine).
- bicuspid (bi·kŭs'pĭd) [L. bi, two, + cuspis, point]: ending in two points, as in bicuspid heart valve, two flaps of tissue guarding opening between left auricle and left ventricle; see also mitral.
- biennial (bi · ěn'í · ăl) [L. bi, two, + annus, year]: occur-

- ring once every two years, as in biennial plant, which flowers and forms seed every second year.
- bioluminescence (bī'ó·lū'mĭ·nĕs'ĕns) [Gr. bios, life, + L. lumen, light]: emission of light by living organisms. biotin (bī'ó·tin): one of the B vitamins.
- blastopore (blăs'tô · pôr): opening connecting archenteron of gastrula with outside; represents future mouth in some animals, future anus in others.
- blastula (blăs'tů·là): stage in early animal development when embryo is a hollow, and in some cases a solid, sphere of cells; the sphere typically is constructed from a single layer of cells.
- bryophyte, Bryophyta (brī'ō·fit) [Gr. bryon, moss, + phyton, a plant]: (1) a moss, liverwort, or hornwort, i.e., any terrestrial green plant which is neither algal nor tracheophytic; (2) phylum name.
- cambium (kăm'bĭ·ŭm) [L., exchange]: embryonic tissue in roots and stems of tracheophytes, giving rise to xylem and phloem (secondary growth).
- carbohydrate, carbohydrase (kär'bö · hí'drāt): (1) an organic compound consisting of a chain of carbon atoms to which hydrogen and oxygen, present in a 2:1 ratio, are attached; (2) an enzyme promoting the synthesis or decomposition of a carbohydrate.
- carnivore, Carnivora (kär'nĭ · vor, kär · nĭv'ŏ · ra) [L. carnivorus, flesh-eating]: (1) any bulk-feeding organism subsisting on animals or parts of animals; (2) an order of mammals; includes cats, dogs, seals, walruses.
- carotene, carotenoids (kăr'ō · tēn, ka · rōt'ē · noid) [L. carota, carrot]: (1) a pigment producing cream-yellow to
 carrot-orange colors; precursor of vitamin A; (2) a
 class of pigments of which carotene is a member.
- catalysis, catalyst, catalytic (kā·tăl'ī·sīs) [Gr. katalysis, dissolution]: (1) acceleration of a chemical reaction by a substance which does not become part of the endproduct; (2) a substance which accelerates a reaction as above; (3) adjective.
- cathepsin (kā·thěp'sĭn): enzyme within cells promoting the synthesis or decomposition of proteins.
- Cenozoic (sē'nö · zō'īk) [Ġr. kainos, recent, + zōē, life]: geological era after the Mesozoic, dating approximately from 75 million years ago to present.
- centriole (sen'tri·ol): cytoplasmic body forming spindle pole during mitosis and meiosis; present in cells of primitive plants and most animals.
- centromere (sĕn'trō·mēr): region on chromosome at which spindle fibril is attached during mitosis and meiosis.

- Cephalochordata, Cephalopoda, cephalothorax (sef'a·lō—) [Gr. kephalē, head]: (1) a subphylum of chordates; the lancelets or amphioxus; (2) a class of mollusks; squids, octopuses, nautiluses; (3) the fused head and thorax in certain arthropods, e.g., crustacea.
- cercaria (sûr·kā'rī·ā) [Gr. kerkos, tail]: a larval stage in the life cycle of flukes; produced by a redia, and infects fish, where it encysts.
- cerebellum (sĕr'é·bĕl'ŭm) [L. dim. of cerebrum]: a part of the vertebrate brain, controlling muscular coordination.
- cerebrum (sĕr'ē·brum) [L., brain]: a part of the vertebrate brain, especially large in mammals; controls many voluntary functions and is seat of higher mental capacities.
- chemosynthesis (kĕm'ö·sin'thė·sis): a form of autotrophic nutrition in certain bacteria, in which energy for the manufacture of carbohydrates is obtained from inorganic raw materials.
- chitin (kī'tĭn): a horny organic substance forming the exoskeleton of arthropods and the epidermal cuticle of many other invertebrates.
- chloroplast, chlorophyll, chlorophyte (klō'rō-) [Gr. chloros, green]: (1) chlorophyll-containing plastid; (2) green light-trapping pigment essential as energy donor in photosynthesis; (3) a green alga, member of the phylum Chlorophyta.
- cholinergic (kö'lin · ûrjik): refers to a type of nerve fiber which releases acetylcholine from the axon terminal when impulses are transmitted.
- Chondrichthyes (kŏn·drĭk'thĭ·ēz) [Gr. chondros, cartilage, + ichthyos, fish]: fishes with cartilage skeleton, a class of vertebrates comprising sharks, skates, rays, and related types.
- Chordata (kôr · dā'tá) [L. chorda, cord]: animal phylum in which all members possess notochord, dorsal nerve cord, and pharyngeal gill slits at least at some stage of the life cycle; four subphyla, the Hemichordata, the Urochordata, the Cephalochordata, and the Vertebrata.
- chorion (kō'rī·ŏn) [Gr.]: one of the extraembryonic membranes in reptiles, birds, and mammals; forms outer cover around embryo and all other membranes and in mammals contributes to structure of placenta.
- chromosome (krō'mō·sōm) [Gr. chroma, color, + soma, body]: gene-containing filamentous body in cell nucleus, becoming conspicuous during mitosis and meiosis; the number of chromosomes per cell nucleus is constant for each species.

chrysophyte, Chrysophyta (kris'ò·fit) [Gr. chrysos, gold, + phyton, a plant]: (1) a golden-brown alga, e.g., a diatom; (2) phylum name.

Ciliophora (sīl'ī·ŏf'òrá) [L. cilium, eyelid, + Gr. phoros, bearing]: a protozoan phylum, in which member organisms possess cilia on body surface; includes ciliates, e.g., Paramecium.

cilium (sĭl'ī·ŭm): microscopic bristlelike process, present on surfaces of many cell types and capable of vibratory motion; functions in cellular locomotion and in creation of currents in water.

coagulation (kö·ăg'ū·lā'shŭn) [L. coagulare]: change in physical state of proteins when internal architecture of protein molecule is destroyed and molecule collapses; gross result is solidification of previously liquid or jellylike proteins.

coccus (kŏk'ŭs), pl. cocci (kŏk'si) [Gr. kokkos, a grain]: a spherical bacterium.

coelenterate, Coelenterata (se · lěn'těr · åt) [Gr. koilos, hollow, + enteron, gut]: (1) an invertebrate animal possessing a body wall of two cell layers, a single alimentary opening, and tentacles with sting cells, e.g., jellyfish, corals, sea anemones, hydroids; (2) phylum name.

coelom (sē'lŏm) [Gr. koilōma, a hollow]: 'body cavity of triploblastic animals, lined entirely by mesoderm.

colloid (kŏl'oid) [Gr. kolla, glue]: a substance divided into fine particles, where each particle is larger than a particle of a true solution but smaller than one in a coarse suspension; a colloid system contains particles of appropriate size and a medium in which the particles are dispersed.

commensal, commensalism (kö·měn'săl, –ĭz'm) [L. cum, with, + mensa, table]: (1) an organism living symbiotically with a host, where the host neither benefits nor suffers from the association; (2) noun.

compound (kom'pound) [L. componere, to put together]: a substance consisting of identical molecules.

conjugation (kŏn•jŏo•gā'shŭn) [L. conjugare, to unite]: a mating process characterized by the temporary fusion of the mating partners; occurs particularly in unicellular organisms.

convergence (kŏn·vūr'jěns) [L. convergere, to turn together]: the evolution of similar characteristics in organisms of widely different ancestry.

corpus luteum (kôr'pŭs lū'tē·ŭm), pl. corpora lutea [L.]: progesterone-secreting bodies in vertebrate ovaries, formed from remnants of follicles after ovulation. cortex (kôr'těks), pl. cortices [L., bark]: the outer tissue layers of an organ or body part, e.g., adrenal cortex, cerebral cortex; also, in plant stems, the tissue between epidermis and phloem.

cotylosaur (kŏt'ī·ló·sôr') [Gr. kotylē, anything hollow, + sauros, lizard]: a member of a group of Permian fossil reptiles, evolved from labyrinthodont amphibian

stock and ancestral to all other reptiles.

crossing over: exchange of parts between two paired chromosomes during meiosis, resulting in unexpected combinations of linked genes within the gametes.

cyanophyte, Cyanophyta (si · ăn'ô · fit) [Gr. kyanos, dark blue, + phyton, plant]: (1) a blue-green alga; (2) phylum name.

cyclosis (sī·klō'sĭs) [Gr. kyklos, circle]: circular stream-

ing and eddying of cellular protoplasm.

cytochrome, cytolysis, cytoplasm, cytosine (sī'tō-, sī tōl'-) [Gr. kytos, vessel]: (1) one of a group of hydrogen carriers in aerobic respiration; transfers hydrogen from flavoprotein to oxygen; (2) dissolution or disintegration of a cell; (3) the protoplasm of a cell between cell membrane and nucleus; (4) a purine, present in nucleotides and nucleic acids.

deamination (dē·ămǐ·nā'shǔn): removal of an amino group, especially from an amino acid.

dehydrogenation, dehydrogenase (dċ hi'drò jĕn - ā'shŭn): (1) removal of hydrogen, as from a molecule; (2) an enzyme promoting dehydrogenation.

denaturation (dē·nă'tūr·ā'shǔn): partial physical disruption of the internal architecture of a protein molecule; denaturation is usually reversible, whereas coagulation is not.

dendrite (dĕn'drīt) [Gr. dendron, tree]: filamentous outgrowth of a nerve cell, conducting nerve impulses from its free end toward the cell body.

denitrify, denitrification (dē·nī'trī·fī): (1) to convert nitrates to ammonia and molecular nitrogen, as by denitrifying bacteria; (2) noun.

desoxyribose (děs·ŏk'sĭ·rī'bōs): a five-carbon sugar having one oxygen atom less than parent-sugar ribose; component of desoxyribose nucleic acid (DNA).

diastole (di·ăs'tô·lē) [Gr. diastolē, moved apart]: phase of relaxation of auricles or ventricles, during which they fill with blood; preceded and succeeded by systole, i.e., contraction.

diffusion (dǐ·fū'zhǔn) [L. diffundere, to pour out]: migration of particles from a more concentrated to a

- less concentrated region; the process tends to equalize concentrations throughout a system.
- diploid (dĭp'loid): a chromosome number twice that characteristic of a gamete of a given species.
- disaccharide (di săk'ā rīd) [Gr. dis, twice, + sakcharon, sugar]: a sugar composed of two monosaccharides; usually refers to 12-carbon sugars.
- divergence (di · vûr'jĕns) [L. divergere, to incline apart]: evolutionary development of dissimilar characteristics in two or more lines descended from the same ancestral stock.
- DNA: abbreviation of desoxyribose nucleic acid.
- dominance: a functional attribute of genes; a dominant gene exerts its full effect regardless of the effect of its allelic partner.
- **DPN:** abbreviation of diphosphopyridine nucleotide; a hydrogen carrier in respiration, transferring hydrogen from fuel either to flavoprotein (aerobic) or to pyruvic acid (anaerobic).
- duodenum (dū'ō·dē'nŭm) [L. duodeni, twelve each]: anterior portion of small intestine, continuation of stomach; bile duct and pancreatic duct open into it.
- echinoderm, Echinodermata (ė·ki'nō·dūrm) [Gr. echinos, urchin, + derma, skin]: (1) one of the spinyskinned animals, i.e., starfishes, sea urchins, brittle stars, sea cucumbers, sea lilies; (2) phylum name.
- ectoderm, ectoparasite (ĕk'tō-) [Gr. ektos, outside]: (1) outer tissue layer of any embryo; (2) a parasite attached to the outside of a host, i.e., to skin, hair, etc.
- egestion (ė• jes chŭn) [L. egerere, to discharge]: the elimination from the alimentary system of unusable and undigested material.
- electrolyte (e · lek'tro · lit) [Gr. elektron, amber, + lytos, soluble]: a substance which ionizes in aqueous solution and so makes possible the conduction of electric current through the solution.
- element (ĕl'é·mĕnt): one of about 100 distinct natural or man-made types of matter, which, singly or in combination, compose all materials of the universe; an atom is the smallest representative unit of an element.
- emulsion (ė·mŭl'shŭn) [L. emulgere, to milk out]: a colloidal system in which both the dispersed and the continuous phase are liquid.
- endergonic (ĕn'dĕr·gŏ·nĭk): energy-requiring, as in a chemical reaction.
- endocrine (ĕn'do · krin) [Gr. endon, within, + krinein,

- to separate]: applied to type of gland which releases secretion not through a duct but directly into blood or lymph; functionally equivalent to hormone producing.
- endoderm, endodermis (ěn'dô·dûrm): (1) inner tissue layer of an embryo; (2) single layer of tissue in a root which separates the cortex from the vascular tissues in the root core; the layer is waterproofed with suberin, but contains nonwaterproofed passage cells.
- endoparasite (čn'dō · păr'ā · sīt): a parasite living in the interior tissues of a host, i.e., not on surface tissues.
- endoplasm, endoplasmic (ĕn'do plăz'm): the inner portion of the cytoplasm of a cell, i.e., the portion immediately surrounding the nucleus; contrasts with ectoplasm or cortex, i.e., the portion of cytoplasm immediately under the cell surface.
- endosperm (ĕn'dö·spûrm): triploid, often nutritive tissue within seed, formed by union of one sperm nucleus with two cells of female gametophyte.
- energy (ĕn'ēr·jī) [Gr. energos, active]: capacity to do work; the time rate of doing work is called power.
- enterocoel, enterocoelomate (ĕn'tēr·ö·sēl') [Gr. enteron, gut, + koilos, hollow]: (1) a coelom formed by the outpouching of a mesodermal sac from the endoderm; (2) an animal possessing an enterocoel, e.g., echinoderms, vertebrates.
- enzyme (ĕn'zim) [Gr. en, in, + zymē, leaven]: a protein produced within an organism, capable of accelerating a particular chemical reaction; a type of catalyst.
- epidermis (ĕp'i·dûr'mis) [Gr. epi, over + derma, skin]: the outermost surface epithelium of an organism.
- epithelium (ĕp'ī·thē'lī·tm) [Gr. epi + thēlē, nipple]: a tissue in which the cells are packed tightly together, leaving little intercellular space.
- esophagus (è·sŏf'á·gŭs) [Gr. oisō, I shall carry, + phagein, to eat]: part of alimentary tract connecting pharynx and stomach.
- estrogen (ĕs'tró• jĕn) [Gr. oistros, frenzy, + genēs, born]: one of a group of female sex hormones, produced by a follicle.
- exergonic (čk'sĕr•gŏ•nĭk): energy-yielding, as in a chemical reaction.
- fat: an organic compound formed by union of glycerin with fatty acids.
- feedback: information passing from an effector to a receptor, i.e., a signal indicating the action performed by an effector.

- fermentation (fûr'mĕn · tā'shŭn): synonym for anaerobic respiration, i.e., fuel combustion in the absence of oxygen.
- fiber (fi'ber) [L. fibra, thread]: a strand or filament of protoplasmic material produced by cells but located outside of cells.
- fibril (fi'bril) [L. dim, of fibra]: a strand or filament of protoplasmic material produced by cells and located within cells.
- fibrin, fibrinogen (fi'brĭn, fī·brĭn'ō·jĕn): (1) coagulated blood protein forming the bulk of a blood clot; (2) a protein present in blood which upon coagulation forms a clot.
- flagellate, flagellum (flăj'ě·lāt, $-\check{u}m$) [L., whip]: (1) equipped with one or more flagella; an organism possessing flagella; (2) a microscopic, whiplike protoplasmic filament serving as locomotor structure in flagellate cells.
- flavoprotein (flā'vô-) [L. flavus, yellow]: a hydrogen carrier in aerobic respiration, derived from riboflavin; passes hydrogen from DPN to the cytochrome system.
- fluorescence (floo'o'res'ens) [L. fluere, to flow]: emission of radiation (light) by a substance which has absorbed radiation from another source.
- follicle (fŏl'í·k'l) [L. folliculus, small ball]: hollow ball of cells in the ovary, containing a maturing egg.
- gamete (găm'ēt) [Gr. gamein, to marry]: reproductive cell which must fuse with another before it can develop; sex cell.
- gametophyte (găm · e'tô · fit): a gamete-producing plant; phase of life cycle in certain plants which alternates with a sporophyte phase.
- ganglion (găng'gli ứn) [Gr., a swelling]: a collection of cell bodies of neurons located outside the brain or the spinal cord.
- Gastropoda (găs · trŏp'ö · da) [Gr. gastros + podos, foot]: a class of mollusks; comprises snails and slugs.
- gastrula, gastrulation (găs'trōo·la, —lā'shŭn): (1) a twolayered, and in most cases later three-layered, stage in the embryonic development of animals; the layers are the ectoderm, mesoderm, and endoderm, and they typically form a hollow sac, the opening being the blastopore; (2) the process of gastrula formation.
- gel (jĕl) [L. gelare, to freeze]: quasi-solid state of a colloidal system, where the solid particles form the continuous phase and the liquid medium forms the discontinuous phase.

- gene (jēn) [Gr. genēs, born]: a segment of a chromosome, definable only in operational terms; repository of a unit of genetic information, contributing to control and maintenance of cell character.
- genome (jēn'ōm): the totality of genes in a haploid set of chromosomes, hence the sum of all different genes in a cell.
- genotype (jčn'ō · tīp): the particular set of genes present in an organism and its cells; the genetic constitution.
- genus (jē'nŭs) [L., race]: a rank category in taxonomic classification, between species and family; a group of very closely related species.
- geotropism (jë·ŏt'rō·pĭz'm) [Gr. gē, earth, + tropē, a turning]: behavior governed and oriented by gravity, i.e., growth of roots toward center of earth.
- germ layer, germ mutation: (1) ectoderm, mesoderm, or endoderm of animal embryo; (2) mutation occurring in a germ cell, i.e., a gamete or other reproductive cell.
- glomerulus (glò·měr'ů·lůs) [L. dim. of glomus, ball]: a small meshwork of blood capillaries found in the cup-shaped capsule of a nephron.
- glucose (gloo'kos) [Gr. gleukos, sweet wine]: a six-carbon sugar; principal form in which carbohydrates are transported from cell to cell in plants and animals.
- glycerin (glĭs'ēr·ĭn) [Gr. glykeros, sweet]: an organic compound possessing a three-carbon skeleton; may unite with fatty acids and form a fat.
- glycogen (gli'kô·jēn): a polysaccharide consisting of some 12 to 18 glucose units; a principal storage form of carbohydrates in animals.
- Golgi body (gôl'jē): a particulate component of cell cytoplasm; probably plays a role in the manufacture of certain cell secretions.
- gonad (gŏn'ăd) [Gr. gonē, generator]: collective term for the reproductive organs of males and females, i.e., testes and ovaries.
- granum (grăn'ūm) [L., grain]: a functional unit of a chloroplast; smallest particle capable of carrying out photosynthesis.
- gymnosperm (jĭm'nō·spûrm) [Gr. gymnos, naked, + sperma, seed]: a plant belonging to a class of seed plants in which the seeds are not enclosed in an ovary; includes the conifers.
- haploid (hăp'loid) [Gr. haploos, single, simple]: a chromosome number characteristic of a mature gamete of a given species.
- hemoglobin (hē'mo glo'bin) [Gr. haima, blood, + L.

globus, globe]: oxygen-carrying constituent of red blood corpuscles; consists of red pigment heme and protein globin.

herbaceous (hûr · bā'shŭs) [L. herbaceus, grassy]: having the character of an herb; contrasts with woody.

herbivore (hûr'bi · vor) [L. herba, herb, + vorare, to devour]: a plant-eating animal.

hermaphrodite (hûr · măf'ro · dit) [fr. Gr. Hermes + Aphrodite]: an organism possessing both male and female reproductive systems.

heterosporous (hět'er · os'porus): producing two different types of spores, viz., microspores and megaspores; microspores give rise to male gametophytes, mega-

spores to female gametophytes.

heterotroph, heterotrophism (het'er · o · trof) [Gr. heteros + trophos, feeder]: (1) an organism which must obtain both inorganic and organic raw materials from the environment; (2) form of nutrition characteristic of heterotrophs.

heterozygote, heterozygous (hět'er · o · zī'got) [Gr. heteros + zygōtos, yoked]: (1) an organism in which a pair of alleles for a given trait consists of different (e.g., dominant and recessive) kinds of genes; (2) adjective.

homosporous (ho · mos'po · rus) [Gr. homos, same]: producing spores all of which are alike; any given spore develops into either a male or a female gametophyte.

homozygote, homozygous (hō'mō · zī'gōt) [Gr. homos, same, + zygōtos]: (1) an organism in which a pair of alleles for a given trait consists of the same (e.g., either dominant or recessive, but not both) kinds of genes; (2) adjective.

humus (hū'mŭs) [L., soil]: the organic portion of soil.

hybrid (hi'brid) [L. hibrida, offspring of tame sow and wild boar]: an organism which is heterozygous for one or more (usually many) gene pairs.

hydrolysis (hi · drŏl'i · sis) [Gr. hydor, water, + lysis, a loosening]: dissolution through the agency of water; especially decomposition of a chemical by the addition of water.

hydroponics (hì'drö · pŏn'īks) [Gr. hydor + ponos, labor]: growing plants without soil, by immersing the roots in a nutrient-rich water medium.

hydroxyl (hi·drŏk'sĭl): OH-, a negatively charged ion released by alkalies in water solution.

hyperparasitism (hī'pēr-) [Gr. hyper, above]: infection of a parasite by one or more parasites.

hypertonic, hypertonicity (hī'pēr·tŏn'ĭk): (1) exerting greater osmotic pull than the medium on the other side of a semipermeable membrane, hence possessing a greater concentration of particles and acquiring water during osmosis; (2) noun.

hypha (hī'fa) [Gr. hyphē, a web]: a filamentous protoplasmic unit of a fungus; a meshwork of hyphae forms a mycelium.

hypothesis (hī·poth'ė·sis) [Gr. hypo, under + tithenai, to put]: a guessed solution of a scientific problem; must be tested by experimentation and, if not validated, must then be discarded.

hypotonic, hypotonicity (hī'pō·tŏn'īk): (1) exerting lesser osmotic pull than the medium on the other side of a semipermeable membrane, hence possessing a lesser concentration of particles and losing water during osmosis; (2) noun.

ichthyosaur (ĭk'thĭ·ō·sôr) [Gr. ichthyos, fish, + sauros, lizard]: extinct marine mesozoic reptile, with fishshaped body and porpoiselike snout.

induction, inductor (in · dŭk'shŭn) [L. inducere, to introduce]: (1) process in embryo in which one tissue or body part causes the differentiation of another tissue or body part; (2) an embryonic tissue which causes the differentiation of another.

ingestion (in · jes'chun) [L. ingerere, to put in]: intake of food from the environment into the alimentary

inorganic (ĭn·ôr·găn'ĭk): applied to noncarbon compounds and those carbon compounds which are derived from or related to carbon dioxide.

insulin (ĭn'sū·lĭn) [L. insula, island]: a hormone produced by the islets of Langerhans in the pancreas; promotes the conversion of blood glucose into tissue glycogen.

integument (ĭn·těg'ů·měnt) [L. integere, to cover]: covering; external coat; skin.

ion, ionization (î'ŏn, -ĭ·zā'shŭn) [Gr. ienai, to go]: (1) an electrically charged atom or group of atoms; (2) splitting of a molecule into ions in water solution.

isotonic (ī'sö·tŏn'īk): exerting the same osmotic pull as the medium on the other side of a semipermeable membrane, hence possessing the same concentration of particles; the net gain or loss of water during osmosis is zero.

lacteal (lăk'të·ăl) [L. lactis, milk]: lymph vessel in a villus of the intestinal wall.

larva (lär'va), pl. larvae (-vē) [L., mask]: period in de-

- velopmental history of animals, between embryo and adult; the larval period begins at hatching and terminates at metamorphosis.
- leucocyte (lū'kò·sīt) [Gr. leukos, white, + kytos, vessel]: a type of white blood cell, characterized by a beaded, elongated nucleus.
- leukemia (lů·kē'mĭ·a): a cancerous condition of blood, characterized by overproduction of leucocytes.
- lichen (li'kěn) [Gr. leichēn]: a symbiotic, mutualistic association of an algal type and a fungal type.
- lignin (lig'nin) [L. lignum, wood]: a substance related to cellulose, present in substantial quantities in wood.
- lipase (li'pās) [Gr. lipos, fat]: an enzyme promoting the conversion of fat into fatty acids and glycerin, or the reverse.
- lipid, lipoid (lĭp'ĭd): (1) fat, fatty, pertaining to fat; (2) fatlike.
- lycopsid (li·kŏp'sĭd) [Gr. lykos, wolf]: a member of a subphylum of tracheophytes; the club mosses.
- lymph (limf) [L. Lympha, goddess of moisture]: the body fluid outside of the blood circulation; leaks out of, and eventually returns to, the blood circulation.
- lymphocyte (lĭm'fô·sīt): a type of white blood cell, characterized by a rounded or kidney-sĥaped nucleus.
- macronucleus (măk'rô·nū'klė·ŭs) [Gr. makros, long, + nucleus, kernel]: a large type of nucleus found in ciliate protozoa; controls all but reproductive functions in these animals.
- madreporite (măd'rė·pò·rīt) [It. madre, mother, + poro, passage]: a sievelike opening on the upper surface of echinoderms, connecting the water-vascular system with the outside.
- maltose (môl'tōs): a 12-carbon sugar formed by the union of two glucose units.
- marsupial (mär·sū'pi·šl) [Gr. marsypion, little bag]: a pouched mammal, member of the mammalian subclass Metatheria.
- medulla (mė·dŭl'a) [L.]: the inner tissue layers of an organ or body part, e.g., adrenal medulla; the medulla oblongata is a region of the hindbrain which connects with the spinal cord.
- medusa (më·dū'sa'): the free-swimming stage in the life cycle of coelenterates; a jellyfish.
- *megaspore* (měg' \dot{a} ·spōr) [Gr. *megas*, great]: a type of spore which develops into a female gametophyte.
- meiosis (mi · ō'sis) [Gr. meioun, to make smaller]: process

- occurring at different points in the life cycles of different organisms in which the chromosome number is reduced by half; compensates for the chromosomedoubling effect of fertilization.
- menstruation (men'stroo · ā'shun) [L. mensis, month]: the discharge of uterine tissue and blood from the vagina, at the end of a menstrual cycle in which fertilization has not occurred.
- meristem (mer'i stem) [Gr. meristos, divided]: embryonic tissue in adult plants, capable of giving rise to additional adult tissues, e.g., apical shoot or root meristem, cambium.
- mesoderm (měs'ó·dûrm) [Gr. mesos, middle, + derma, skin]: the middle tissue layers of an embryo, between ectoderm and endoderm.
- mesogloea (měs'ō glē'à) [Gr. mesos + gloios, glutinous substance]: the jellylike layer between the ectoderm and endoderm of coelenterates and comb jellies.
- mesophyll (měs'ò·fil) [Gr. mesos + phyllon, leaf]: tissue in the interior of leaves, composed of chlorophyll-containing cells arranged either into compact layers (palisade mesophyll) or into loose aggregations (spongy mesophyll).
- metabolism (mě·tăb'ô·lĭz'm) [Gr. metabolē, change]: a group of life-sustaining processes including principally nutrition, production of energy (respiration), and synthesis of more protoplasm.
- metamorphosis (mět'à·môr'fò·sīs) [Gr. metamorphoun, to transform]: the transformation of a larva into an adult.
- metaphase (mět'ă·fāz) [Gr. meta, between]: a stage during mitotic cell division in which the chromosomes line up in a plane at right angles to the spindle axis.
- Metaphyta (mět'á · fi'tá) [Gr. meta, after, later + phyton, plant]: a major group of plant organisms, comprising the bryophytes and the tracheophytes.
- Metazoa (mět'á·zō'á) [Gr. meta + zōion, animal]: a major group of animals, viz., multicellular animals.
- micron (mi'kron), pl. microns, micra [Gr. mikros, small]: one-thousandth part of a millimeter, a unit of microscopic length.
- micronucleus (mī'krö·nū'klö·ŭs): a small type of nucleus found in ciliate protozoa; controls principally the reproductive functions of these organisms.
- microsome (mī'krô·sōm) [Gr. soma, body]: a particulate constituent of cytoplasm; contains RNA and is the site of protein synthesis.

- microspore (mī'krō·spōr): a type of spore which develops into a male gametophyte; syn. pollen.
- mimicry (mim'ik · ri) [Gr. mimos, mime]: the superficial resemblance of certain animals, particularly insects, to other more powerful or more protected ones, resulting in a measure of protection for the mimics.
- miracidium (mi'ră·sĭd'i·ŭm): a larval stage in the life cycle of flukes; develops from an egg and gives rise in turn to numerous sporocyst larvae.
- mitochondrion (mī'to kon'drī on) [Gr. mitos, thread, + chondros, grain]: a particulate constituent of cytoplasm; the site of respiration.
- mitosis (mi·tô'sis) [Gr. mitos, thread]: a form of cell division characterized by complex chromosome movements and exact chromosome duplication.
- mitral (mi'trăl) [fr. miter]: applied to valve between left auricle and ventricle of heart; syn. bicuspid.
- modulator (mŏd'û·lā'tēr): general term for one of the components of steady-state control systems; receives and interprets signals from a receptor and selects and sends out signals to an effector.
- molecule (möl'é·kūl) [L. moles, mass]: the smallest whole unit of a compound; consists of two or more atoms of the same or of different elements.
- mollusk, Mollusca (mŏl'ŭsk, mŏ·lŭs'ka) [L. molluscus, soft]: (1) a member of the phylum Mollusca; (2) a phylum of schizocoelomate animals; unsegmented, body composed of visceral mass, foot, and shell; comprises chitons, snails, clams, squids, and others.
- monosaccharide (mŏn'ò·săk'à·rīd) [Gr. monos + sakcharon, sugar]: a simple sugar, which cannot be decomposed into smaller sugar molecules; five- and sixcarbon sugars are monosaccharides.
- morphology (môr fôl'ô jī) [Gr. morphē + logos, study]: the study or science of structure, at any level of organization; e.g., cytology, study of cell structure; histology, study of tissue structure; anatomy, study of gross structure of organisms.
- mucosa (mt · kō'sa') [L. mucosus, mucus]: a mucussecreting membrane, e.g., the inner lining of the intestine.
- mutation (mū·tā'shŭn) [L. mutare, to change]: a stable change of a gene, such that the changed condition is inherited by offspring cells.
- mycelium (mi sē'li · um) [Gr. mykēs, mushroom]: the vegetative portion of a fungus, consisting of a meshwork of hyphae.

- Mycophyta (mī'kò · fī'tā) [Gr. mykēs + phyton, plant]: the plant phylum comprising the fungi.
- myelin (mi'e·lin) [Gr. myelos, marrow]: a fatty material which surrounds the axons of nerve cells in the central nervous system.
- nekton (něk'tŏn) [Gr. nēktos, swimming]: collective term for the actively swimming organisms in the ocean.
- nematode (něm'á·tōd) [Gr. nēmatos, thread]: a roundworm, member of the pseudocoelomate phylum Nematoda.
- nephric, nephron (něf'rik, -rŏn) [Gr. nephros, kidney]:

 pertaining to a nephron;
 a functional unit of the vertebrate kidney, consisting of glomerulus, capsule, convoluted tubules, Henle's loop, and collecting tubule.
- neuron (nū'rŏn) [Gr., nerve]: nerve cell, including cell body, dendrites, and axons.
- nitrify, nitrification (nī'trī·fī, -fī, ·kā'shŭn): (1) to convert ammonia and nitrites to nitrates, as by nitrifying bacteria; (2) noun.
- node (nod) [L. nodus, knot]: in plants, a joint of a stem; place where branches and leaves are joined to stem.
- notochord (nō'tō kôrd) [Gr. nōton, the back, + L. chorda, cord]: longitudinal elastic rod of cells serving as internal skeleton in the embryos of all chordates and in the adults of some; in most adult chordates the notochord is replaced by a vertebral column.
- nucleic acid (nti·kle'ik): one of a class of molecules composed of joined nucleotide complexes; the principal types are desoxyribose nucleic acid (DNA), found only in cell nuclei (chromosomes), and ribose nucleic acid (RNA), found both in cell nuclei (chromosomes and nucleoli) and in cytoplasm (e.g., microsomes).
- nucleolus (nū · klē'ō · lūs): an RNA-containing body within the nucleus of a cell; a derivative of chromosomes.
- nucleoplasm (nū'klė·ȯ·plăz'm): the protoplasm which forms a nucleus; also specifically the nuclear sap.
- nucleoprotein (nū'klē·ò-): a supermolecule composed of nucleic acid and protein; occurs in two variant forms, according to whether the nucleic acid portion is DNA or RNA.
- nucleotide (nū'klė·ȯ·tid): a molecule consisting of joined phosphate, five-carbon sugar (either ribose or desoxyribose), and a purine or a pyrimidine (adenine, or guanine, or uracil, or thymine, or cystosine).

- nucleus (nū'klė·ŭs) [L., a kernel]: a body present in all cell types except the bacteria and the blue-green algae and consisting of external nuclear membrane, interior nuclear sap, and chromosomes and nucleoli suspended in the sap.
- omnivore (ŏm'nĭ·vōr) [L. omnis, all, + vorare, to devour]: an animal which may subsist on plant foods, animal foods, or both.
- organ (ôr'găn) [fr. Gr. organon]: a group of different tissues joined structurally and cooperating functionally to perform a composite task.
- organic (ôr·găn'īk): applied to molecules containing carbon, except those which are derivatives of carbon dioxide; virtually all organic molecules contain linked carbon atoms.
- organism (ôr'găn · ĭz'm): an individual living creature, either unicellular or multicellular.
- osmosis (ŏs·mō'sīs) [Gr. ōsmos, impulse]: the process in which water migrates through a semipermeable membrane, from the side containing a lesser concentration of particles to the side containing a greater concentration; migration continues until particle concentrations are equal on both sides (i.e., until the relative concentrations of water are the same).
- Osteichthyes (ŏs·tė·ĭk'thĭ·ēz) [Gr. osteon, bone]: a class of vertebrates, comprising the bony fishes.
- ovary (ō'va·rī) [L. ovum, egg]: the reproductive organ of female organisms; in plants, contains one or more megaspores (hence female gametophytes and eggs); in animals, manufactures eggs.
- ovulation (ō'vû·lā'shǔn): expulsion of an egg from the ovary and deposition of egg into the oviduct.
- oxidation (ŏk'sĭ·dā'shŭn): internal rearrangement of a molecule so as to create a high-energy bond; often achieved by dehydrogenation.
- paleontology (pā'lė·ŏn·tŏl'ò·jĭ) [Gr. palaios, old, + onta, existing things]: study of past geological times, principally by means of fossils.
- Paleozoic (pā'lė·ȯ·zō'īk) [Gr. palaios + zōē, life]: the geological era between the pre-Cambrian and the Mesozoic, dating approximately from 500 to 200 million years ago.
- parasite (păr'a · sit) [Gr. para + sitos, food]: an organism which lives symbiotically on or within a host organism, more or less detrimental to the host.
- parasympathetic (păr'a · sĭm'pa · thĕt'ĭk): applied to a

- subdivision of the autonomic nervous system; centers are located in brain, most anterior part of spinal cord, and most posterior part of spinal cord.
- parenchyma (på · rěng'kǐ · må) [Gr. para + en, in, + chein, to pour]: in plant stems and roots, the tissue of the pith and the cortex.
- parthenogenesis (pär'thė · nō · jěn'ė · sīs) [Gr. parthenos, virgin, + genēs, born]: development of an egg without fertilization; occurs naturally in some organisms (e.g., rotifers) and may be induced artificially in others (e.g., frogs).
- pathogenic (păth'ō · jĕn'ĭk) [Gr. pathos, suffering, + genēs]: disease-producing, e.g., many bacteria, fungi, and other parasites.
- pepsin (pěp^fsĭn) [Gr. peptein, to digest]: a proteindigesting enzyme present in gastric juice.
- perennial (per · en'ī · al) [L. perennis, throughout a year]: a plant which lives continuously throughout the year and persists in whole or in part from year to year.
- peristalsis (pěr'i stăl'sĭs) [Gr. peristaltikos, compressing]: successive contraction and relaxation of tubular organs such as the alimentary tract, resulting in a wavelike propagation of a transverse constriction.
- permeability (pûr'më·a·bĭl'ī·tī) [L. permeare, to pass through]: penetrability, as in membranes which let given substances pass through.
- petiole (pět'ĭ·ōl) [L. petiolus, little foot]: leafstalk; the slender stem by which a leaf blade is attached to a branch or a stem.
- pH: a symbol denoting the relative concentration of hydrogen ions in a solution; pH values run from 0 to 14, and the lower the value, the more acid is a solution, i.e., the more hydrogen ions it contains.
- Phaeophyia (fē'ò·fi't·à): the phylum of brown algae. pharynx (făr'ingks) [Gr.]: the part of the alimentary tract between mouth cavity and esophagus; it is also part of the air channel from nose to larynx.
- phenotype (fē'nō·tip) [Gr. phainein, to show]: the physical appearance of an organism resulting from its genotype, i.e., its genetic constitution.
- phloem (flo'em) [Gr. phloos, bark]: one of the conducting tissues in tracheophytic plants; consists of sieve tubes and companion cells and transports organic nutrients both up and down.
- phosphorylation (fŏs'fŏ·rĭ·lā'shŭn): the addition of a phosphate group (for example, —H₂PO₃) to a compound.

- photolysis (fo tol'i sis) [Gr. phōtos, light, + lysis, a loosening]: a component process of photosynthesis in which water is split into hydrogen and oxygen through the energy of light.
- photosynthesis (fö'tö·sĭn'thė·sĭs) [Gr. phōtos, light, + syn, together, + tithenai, to place]: process in which energy of light and chlorophyll are used to manufacture carbohydrates out of carbon dioxide and water.
- phototropism (fö·töt'rö·pĭz'm) [Gr. phōtos + tropē, a turning]: behavior oriented by light, e.g., growth of plant stems toward light source.
- phylum (fi'lm), pl. phyla [Gr. phylon, race, tribe]: a category of taxonomic classification, between class and kingdom.
- physiology (fiz'ī·ŏl'ō·jĭ) [Gr. physis, nature, + logos, study]: study of living processes, activities, and functions generally; contrasts with morphology, the study of structure.
- pistil (pis'til) [L. pistulus, a pestle]: the female reproductive parts of a flower; consists of stigma, style, and ovary.
- pituitary (pi·tū'i·tēri) [L. pituita, phlegm]: a composite endocrine gland in vertebrates, attached ventrally to the brain; composed of anterior, intermediate, and posterior lobes, each representing a functionally separate gland.
- placenta (pla · sĕn'ta) [L., cake]: a tissue complex formed in part from the inner lining of the uterus and in part from the chorion of the embryo; develops in most mammals and serves as mechanical, metabolic, and endocrine connection between the adult female and the embryo during pregnancy.
- placoderm (pläk'ò · dûrm) [Gr. plakos, flat plate, + derma, skin]: a member of a class of Devonian vertebrates (fishes), all now extinct; ancestral to cartilage and bony fishes.
- planarian (pla · nâr'ĭ · ăn) [L. planarius, level]: any member of the class of free-living flatworms.
- plankton (plăngk'tŏn) [Gr. planktos, wandering]: collective term for the passively floating or drifting flora and fauna of a body of water; consists largely of microscopic organisms.
- plastid (plăs'tid) [Gr. plastēs, a molder]: a cytoplasmic, often pigmented body in plant cells; plastids which contain chlorophyll are called chloroplasts.
- Platyhelminthes (plāt'ī·hěl·mĭn'thēz) [Gr. platys, flat, + helminthos, worm]: flatworms, a phylum of acoelomate animals; comprises planarians, flukes, and tapeworms.

- polyp (pŏl'īp) [L. polypus, many-footed]: the sessile stage in the life cycle of coelenterates; a sea anemone.
- polysaccharide (pŏl'ĩ·săk'ā·rīd): a carbohydrate composed of many joined monosaccharide units, e.g., glycogen, starch, cellulose, all formed out of glucose units.
- Porifera (po · rĭf'er · a) [L. porus, pore, + ferre, to bear]: the phylum of sponges.
- progesterone (pró·jes'ter·on): hormone secreted by the corpus luteum and the placenta; prepares the uterus for the reception of a fertilized egg and later maintains the capacity of the uterus to hold the embryo and fetus.
- prophase (prō/fāz'): a stage during mitotic cell division, in which the nuclear membrane dissolves, chromosomes become distinct, and a spindle forms.
- prosimian (prō · sim'ī · an) [L. pro, before, + simia, ape]:
 an ancestral primate and certain of primitive living primates, e.g., a lemur, a tarsier.
- protein (protevin) [Gr. proteios, primary]: one of a class of organic compounds composed of many joined amino acids.
- proteinase (prō'té·ĭn·ās): an enzyme which promotes the conversion of a protein into smaller units, e.g., amino acids, or the reverse; also called protease.
- prothrombin (pro throm'bin) [L. pro + Gr. thrombos, clot]: a constituent of blood plasma; converted to thrombin by thrombokinase in the presence of calcium ions, and so contributes to blood clotting.
- Protista (prô·tĭs'tá) [Gr. prōtistos, first]: ancient nucleated organisms and their descendants, comprising the algae, fungi, slime molds, and protozoa.
- protoplasm (prô'tô · plăz'm) [Gr. protos, first, + plasma, form, mold]: synonym for living matter, living material, or living substance.
- protozoon (prō'tō · zō'ŏn) [Gr. protos + zōion, animal]: a unicellular animal; a member of either the phyla Sarcodina, Ciliophora, Sporozoa, or Zooflagellata.
- pseudocoel, pseudocoelomate (sū'dò · sēl, --ó · māt) [Gr. pseudēs, false]: (1) an internal body cavity lined not by mesoderm but by ectoderm and endoderm; (2) an animal possessing a pseudocoel, e.g., rotifers, roundworms.
- Psilopsida (si·lŏp'si·dà) [Gr. psilos, bare]: a subphylum of tracheophytes; includes the earliest, now extinct, representatives of the vascular plants; evolved probably from green algae, and in turn ancestral to all living tracheophytes.

- Pteropsida (të rop'si dà) [Gr. pteridos, fern]: a subphylum of tracheophytes; includes ferns and all seed plants, i.e., large-leafed vascular plants; probably evolved from psilopsids.
- Pyrrophyta (pir'ò·iit·à) [Gr. pyr, fire, + phyton, plant]: phylum of algae to which the dinoflagellates belong.
- receptor (rė·sĕp/tēr) [L. recipere, to receive]: general term for one of the components of a steady-state control system; it is sensitive to a stimulus and in turn transmits a signal to the modulator.
- recessive (re. ses'iv) [L. recedere, to recede]: a functional attribute of genes; the effect of a recessive gene is masked if the allelic gene is dominant.
- redia (rē'dĭ·a): a larval stage in the life cycle of flukes; produced by a sporocyst larva, and in turn gives rise to many cercariae.
- reflex (refleks) [L. reflectere, to bend back]: the unit action of the nervous system; consists of stimulation of a sense receptor, interpretation and emission of nerve impulses by a neural center, and execution of a response by an effector organ.
- renal (rē'nāl) [L. renes, kidneys]: pertaining to the kidney.
- rennin (rĕn'īn) [Middle English rennen, to run]: an enzyme present in gastric juice; promotes the coagulation of milk.
- respiration (res'pi·ra'shun) [L. respirare, to breathe]: the liberation of metabolically useful energy from fuel molecules within cells; may occur anaerobically or aerobically.
- Rhodophyta (ro'dŏf'i·ta) [Gr. rhodon, rose, + phyton, plant]: the phylum of red algae.
- Rotifera (rô · tǐffer · a) [L. rota, wheel, + ferre, to bear]:
 a phylum of microscopic pseudocoelomate animals, characterized by whorls of motile bristles around the mouth.
- salt (sôlt): an interaction product of an acid and a base. saprophyte (săp'rô·fit) [Gr. sapros, rotten]: an organism subsisting on dead or decaying matter.
- Sarcodina (sär'kö·di'na) [Gr. sarkos, flesh]: a phylum of protozoa; includes amoebae, foraminifera, radiolaria, and others.
- schizcocoel, schizocoelomate (skĭz'ô·sēl) [Gr. schizein, to split]: (1) a coelum formed by a splitting of embryonic mesoderm; (2) an animal possessing a schizocoel, e.g., mollusks, annelids, arthropods.

- Schizophyta (ski · zŏf'i · ta) [Gr. schizein + phyton, plant]: the phylum of bacteria.
- semiherbaceous (sĕm'ī·hūr·bā'shŭs) [L. semi, half, + herbaceus, grassy]: applied to stem type intermediate in character between woody and herbaceous types; young parts of stem possess strips of cambium, as in herbaceous types; old parts possess tube of cambium, as in woody types.
- semipermeable (sĕm'ĭ · pûr'mė · a · b'l): permeable to small particles (e.g., proteins, fat molecules).
- sepal (sē'păl): one of the leaves in the outermost whorl of a flower.
- serum (sēr'ŭm) [L.]: the fluid remaining after removal of fibrinogen from blood plasma.
- simian (sĭm'ī·ăn) [L. simia, an ape]: pertaining to monkeys; also used as noun.
- sol (sŏl): quasi-liquid state of a colloidal system, where water forms the continuous phase and solid particles the dispersed phase.
- somatic (sō·măt'īk) [Gr. sōma, body]: pertaining to the body, e.g., somatic mutation, stable gene change occurring in a cell of the body generally, rather than in a reproductive, or germ, cell.
- species (spē'shīz), pl. species (spē'shēz) [L., kind, sort]: a category of taxonomic classification, below genus rank, defined by breeding potential or gene flow: interbreeding and gene flow occur among the members of a species but not between members of different species.
- Sphenopšida (sfē·nŏp'sĭ·dā) [Gr. sphēn, a wedge]: a subphylum of tracheophytes; includes the horsetails.
- spirillum (spi·rĭl'um) [L. spirilla, little coil]: any bacterium possessing a wavy, coiled, or spiral body.
- spore (spōr) [Gr. spora, a seed]: a reproductive cell of plants, capable of developing into an adult directly.
- sporocyst (spō'rō·sist): a larval stage in the life cycle of flukes; produced by a miracidium larva and in turn gives rise to many rediae.
- sporophyte (spōr'ó·fit): a spore-producing plant; phase of life cycle in certain plants which alternates with a gametophyte phase.
- Sporozoa (spō'rō·zō'a): a phylum of parasitic protozoa; most familiar member is the organism which produces malaria.
- stamen (stā'měn) [L., a thread]: a male reproductive part of a flower; consists of stalk and anther.
- stigma (stig'ma) [Gr., the mark of a pointed instrument]: the uppermost part of a pistil, serving as landing platform for pollen grains.

- stimulus (stīm'û·lŭs) [L.]: any environmental change which activates a receptor.
- stoma (stō'ma), pl. stomata [Gr., a mouth]: a microscopic opening in the epidermis of a leaf, formed by a pair of guard cells; interconnects the interior air spaces of a leaf with the external atmosphere.
- style (stil) [Gr. stylos, a pillar]: stalklike part of a pistil which connects the stigma with the ovary.
- symbiont, symbiosis (sim'bi·ŏnt, sim'bi·ō'sīs) [Gr. syn, with, + bios, life]: (1) an organism which lives in symbiotic association with another; (2) the intimate living together of two organisms of different species, for mutual or one-sided benefit; the principal variants are mutualism, commensalism, and parasitism.
- sympathetic (sĭm'pa' · thĕt'īk): applied to a subdivision of the autonomic nervous system; centers are located in the mid-portion of the spinal cord.
- synapse (si · naps') [Gr. synapsis, conjunction]: the microscopic space between the axon terminal of one neuron and the dendrite terminal of another adjacent neuron.
- syncytium (sǐn·sīsh'ĩ·ữm) [Gr. syn + kytos, vessel]: a multinucleate tissue or mass of protoplasm without internal cell boundaries.
- systole (sĭs'tô·lē) [Gr. syn + stellein, to place]: the phase of contraction of auricles or ventricles during which blood is pumped forward along the circulation path.
- taiga (ti'ga) [Russ.]: terrestrial habitat zone characterized by large tracts of coniferous forests, long, cold winters, and short summers; bounded in the north by tundra; found particularly in Canada, northern Europe, and Siberia.
- taxonomy (tăks · ŏn'ō · mĭ) [Gr. taxis, arrangement, + nomos, law]: plant and animal classification, based as far as possible on natural relationships.
- telophase (těl'ó·fāz) [Gr. telos, end]: a stage in mitotic cell division during which cell cytoplasm cleaves into two and nuclei form in daughter cells.
- template (těm'plět): a pattern, or mold, guiding the formation of a duplicate; term applied especially to gene duplication, which is explained in terms of a template hypothesis.
- testis (těs'tĭs) [L.]: male reproductive organ; produces sperms.
- thrombin (throm'bin) [Gr. thrombos, clot]: substance participating in blood clotting; formed from prothrombin, and in turn converts fibrinogen into fibrin.
- thyroxin (thi·rŏk'sin): the hormone secreted by the thyroid gland.

- tissue (tish'ū) [L. texere, to weave]: an aggregate of cells of similar structure performing similar functions; the cells may be packed tightly or may be separated by greater or lesser amounts of intercellular material.
- trachea, tracheal (trā'kė·ā) [Gr. trachys, rough]: (1) airconducting tube, as in windpipe of mammals and breathing system of insects; (2) adjective.
- tracheophyte, Tracheophyta (trā'kė·ô·fit): (1) a vascular plant, i.e., one possessing xylem and phloem; term applicable to all plants other than algae, fungi, and bryophytes; (2) phylum name.
- transduction (trăns · dŭk'shŭn): transfer of genetic material from one bacterium to another through a virus. translocation (trăns'lô · kā'shŭn): transport of organic substances in phloem.
- transpiration (trăn'spř·rā'shǔn) [L. trans, across, + spi-rare, to breathe]: evaporation of water from leaves or other exposed surfaces.
- tricuspid valve (tri·kŭs'pĭd) [L. tri, three, + cuspis, a point]: valve consisting of three flaps guarding opening between right auricle and right ventricle of heart.
- trophic (trôf'îk) [Gr. trophos, a feeder]: pertaining to nutrition, i.e., autotrophic, heterotrophic.
- tropic, tropism (trŏp'ĭk) [Gr. tropē, a turning]: (1) pertaining to behavior or action brought about by specific stimuli; i.e., phototropic (light-oriented, growing), gonadotropic (stimulating the gonads); (2) noun.
- trypsin (trip'sin) [Gr. tryein, to wear down]: enzyme promoting digestion of proteins; acts in small intestine, but produced as inactive trypsinogen by pancreas.
- tundra (toon'dra) [Russ.]: terrestrial habitat zone, between taiga in south and polar region in north, characterized by absence of trees, short growing season, and frozen ground during much of the year.
- turgor (tûr'gŏr) [L. turgere, to swell]: the distention of a plant (or animal) cell by its fluid content.
- umbilicus (ŭm·bĭl'ī·kŭs) [L.]: the navel; during pregnancy, an umbilical cord connects the placenta with the offspring, and the point of connection with the offspring later becomes the navel.
- urea (ti·rē'a) [Gr. ouron, urine]: an organic compound formed in the liver out of ammonia and carbon dioxide and excreted by the kidneys; represents principal means of ammonia disposal in mammals and some other animal groups.
- ureter (û · rê'têr) [fr. Gr.]: duct carrying urine from a kidney to the urinary bladder.

- urethra (û·rē/thra) [fr. Gr.]: duct carrying urine from the urinary bladder to the outside of the body; in the males of most mammals, the urethra also leads sperms to the outside during copulation.
- uterus (ū'tēr·ŭs) [L., womb]: enlarged region of the female reproductive duct in which offspring develops during pregnancy and receives maternal nourishment.
- vacuole (văk'û·ōl) [L. vacuus, empty]: a small, usually spherical space within a cell, bounded by a membrane and containing fluid, solid matter, or both.
- vagus (vā'gŭs) [L., wandering]: the tenth cranial nerve; it is a mixed nerve, innervating many organs in the chest and the abdomen.
- vascular bundle (văs'kû·lêr) [L. vasculum, small vessel]: a small group of xylem and phloem channels, with and without cambium, traversing roots, stem, and leaves; characteristic of nonwoody tracheophytes.
- ventricle (ven'trī·k'l) [L. ventriculus, the stomach]: a chamber of the heart which receives blood from an auricle and pumps out blood from the heart.
- villus (vīl'ūs), pl. villi [L., a tuft of hair]: a tiny fingerlike process projecting from the intestinal lining into the cavity of the gut; contains blood and lymph capillaries and is bounded by the intestinal mucosa.

- virus (vi'rŭs) [L., slimy liquid, poison]: a submicroscopic noncellular particle, composed of a nucleoprotein core and a protein shell; parasitic, and within a host cell it may reproduce and mutate.
- vitamin (vi'ta·min) [L. vita, life]: one of a class of organic substances contributing to the formation or action of cellular enzymes; synthesized by plants, but animals cannot manufacture many vitamins, and these must be supplied prefabricated in food.
- xanthophyll (zăn'thô · fil) [Gr. xanthos, yellow, + phyllon, leaf]: one of a group of yellow pigments found widely among plants and animals; the xanthophylls are members of the carotenoid group of pigments.
- xylem (zi'lèm) [Gr. xylon, wood]: tissue in plants which conducts water from roots to leaves; consists of columns of tracheids or of uninterrupted cellulose channels (xylem vessels); derived from cambium and in bulk represents wood.
- zygote [zī'gōt) [Gr. zygōtos, yoked]: the cell resulting from the sexual fusion of two gametes; a fertilized egg.

INDEX

Amino group, 26

A-V valves, 309 Absorption, intestinal, 224 from soil, 200 Abyssal plain, 76 Acetic acid, 257 Acetylcholine, 329 Acid, definition of, 102 Acoelomates, 170 Adaptation, 45 and evolution, 438 and sex, 360 Adaptive radiation, 439 Adenine, 290 Adenosine phosphates, 249 ADP, 249 Adrenal, 301 Adrenalin in nerve, 329 Adrenergic nerves, 329 Aerobic respiration, 41, 253 Air, 39 Alcohol in respiration, 255 Algae, 126 red, 131 reproduction of, 374 Alimentation, 164, 218 Alkali, definition of, 102 Allantois, 405 Alleles, 416 Alternation of generations, 374, 377 Alveolus, 237 Amino acids, 98 in blood, 230 essential, 270

origin of, 25

Ammonia, in decay, 90 origin of, 22 Amnion, 404 Amphibia, 193 evolution of, 453 Amphioxus, 188 Anaerobic respiration, 41, 254 Anaphase, 351 Angiosperms, 146 reproduction of, 386 Animals, camouflage of, 68 characteristics of, 164 hormones of, 298 migration of, 64 nutrition of, 216 organ systems of, 165 origin of, 37 reproduction of, 393 Annual plants, 148 Annual rings, 155 Anther, 388 Antheridium, 361 Anthocyanin, 207 Aorta, 241, 309 Apes, 464 Apical meristems, 151, 156 Appetite, 218 Aqueous humor, 334 Archegonium, 361 Artery, 241 Arthropods, 180, 181 Ascus, 139 Aster, 351

Atmosphere, ancient, 22 modern, 88
Atoms, 18
ATP, 249
uses of, 264
Atrium, 191
Auricles, 309
Auriculoventricular (A-V) valves, 309
Australopithecus, 466
Autosome, 422
Autotrophs, 197
Auxins, 296
Axons, 321

Bacillus, 124 Bacteria, 123 denitrifying, 90 nitrifying, 90 nitrogen-fixing, 89 origin of, 35 reproduction of, 372 Bacteriochlorophyll, 124 Bacteriophage, 70, 424 Balance senses, 339 Bark, 155 Basidium, 140 Basilar membrane, 340 Bee society, 59 Benthos, 76 Bicarbonate, 244 Biennials, 148 Bile, 220

Bioelectricity, 267 Biology, definition of, 13 Bioluminescence, 267 Birds, 193 Bladder, 315 Blastopore, 401 Blastula, 400 Blind spot, 336 Blood, circulation of, 308 clotting of, 308 in food transport, 226 in gas transport, 241 Blood cells, 305 Blood plasma, 304 Blood platelets, 307 Blood pressure, 313 Blood serum, 308 Bluegreen algae, 35, 125 Bond energy, 19, 247 Bony fishes, 192 Brain, 341 Breathing patterns, 233 Breathing process, 237 Breathing system, 234 Bronchus, 237 Brown algae, 130 Brownian motion, 105 Bryophytes, 143 reproduction of, 379 Bundle of His, 312

Cambium, 153 Cambrian, 449 Carbohydrase, 105, 220 Carbohydrate, 25, 97 respiration of, 258 Carbon, properties of, 23 in protoplasm, 95 Carbon cycle, 88 Carbon dioxide, in breathing, 241 fixation of, 209 Carboniferous, 454 Carnivore, 164 Carotene, 128, 206 Carotenoids, 206 Cartilage, 191 Catalyst, 103 Cathepsins, 270 Cell, origin of, 31 reproduction of, 351 structure of, 110 Cell membrane, 111

Cell theory, 110 Cell wall, 116 Cellulose, 98, 125 Cenozoic, 454 Centipedes, 185 Centriole, 114, 351 Centromere, 352 Cerebellum, 343 Cerebrum, 343 Chemosynthesis, 37, 198 Chitin, 116, 180 Chlorophyll, 38, 125, 207 Chlorophytes, 127 Chloroplast, 114, 206 Cholinergic nerves, 329 Chordates, 188 Chorion, 404 Choroid, 334 Chromosomes, 111 in heredity, 414 Chrysophytes, 129 Ciliates, 135 Circulation of blood, 309 Citric acid cycle, 260 Clams, 175 Class, taxonomic, 120 Cleavage of egg, 400 Climate, 85 Climax community, 66 Closed system, 84, 279 Clotting of blood, 307 Coagulation, 99 Coccus, 124 Cochlea, 339 Coelenterates, 170 Coelom, 167 Collar cells, 168 Colloid, 105 Combustion, respiratory, 256 Commensalism, 69 Community, 48, 65 Companion cell, 153 Compound, chemical, 18 Conditioned reflex, 344 Cones in eye, 336 Conjugation, 359 Continental shelf, 76 Control, experimental, 7 of metabolism, 282 Control system, 278 Convergence, evolutionary, 441 Cork cambium, 155 Cornea, 334

Corpus luteum, 397 Cortex, adrenal, 301 cerebral, 343 in plants, 152 Corti, organ of, 340 Cotylosaurs, 455 Cro-Magnon, 468 Cross-fertilization, 362 Crossing over, 420 Crustacea, 182-183 Currents, oceanic, 86 Cutaneous senses, 330 Cuticle, 116 Cyanophytes, 125 Cyclosis, 114 Cytochrome system, 254 Cytoplasm, 111 Cytosine, 290

Darwin, theory of, 431 Deamination, 229 Decay, 89 Deciduous plants, 82, 149 Decomposition, chemical, 21 Dehydrogenation, 248 Denaturation, 99 Dendrite, 321 Denitrification, 90 Desert, 81 Desoxyribose, 99 Development, 397 Devonian, 453 Diaphragm, 237 Diastole, 310 Diatoms, 77 Differentiation, 398 Diffusion, 106 in phloem, 204 in root, 201 Digestion, 220 Dinoflagellates, 77, 129 Dinosaurs, 455, 456 Diploidy, 363 Disaccharide, 97 Divergence, evolutionary, 441 Division, taxonomic, 120 DNA, 99, 289 distribution of, 112 duplication of, 291 Domestication, 437 Dominance, genetic, 416 DPN, 254

Ear, 339
Earthworms, 178
Eating, 36
control of, 219
Echinoderms, 187
Ectoderm, 167, 401
Ectoparasite, 70
Effector, 278
Egg (gamete), 356
Electric organs, 267
Electric organs, 207
,
Elements, chemical, 18, 96
Embryo, 393
development of, 397
induction in, 403
Endergonic reactions, 21
Endocrine glands, 273, 298
Endoderm, 167, 401
Endodermis, 157
Endoparasite, 71
Endoplasmic reticulum, 116
Endosperm, 390
Energy, 19
in bonds, 247
production of, 246
transfer of, 250
utilization of, 264
Enterocoelomates, 186
Environment, global, 84
Enzymes, 27, 103
action of, 104
digestive, 220
specificity of, 104
types of, 105
Epidermis, 151
Era, geologic, 447
Estrogen, 396
Euglenophytes, 128
Eurypterid, 449
Eustachian tube, 235
Evidence, nature of, 7
Evolution, 30
of animals, 448
bush pattern of, 123
characteristics of, 438
evidence for, 437
forces of, 433
genetic basis of, 435
historical background of, 430
of man, 458 mechanism of, 433
past course of, 446
of plants, 448

Evolution, rates of, 438
Excretion, 315
Exergonic reactions, 21
Exhalation, 238
Exocrine gland, 273
Experiment, 6
Extinction, evolutionary, 440
Extraembryonic membranes, 404
Eye, 334
compound, 181
development of, 401
simple, 181

Family, 48, 63 taxonomic, 120 Fat, 27, 98 Fatty acid, 25, 98 Feces, 225 Feedback, 281 Fermentation, 255 Ferns, 145 reproduction of, 381 Fertilization, 357 Fibrin, 308 Fishes, 191 evolution of, 452 Fission, cellular, 351 Flatworms, 172 Flavoprotein, 254 Flower, 387 Food, 29 absorption of, 223 intake of, 218 manufacture of, 205 Food pyramid, 67 Foraminifera, 134 Forest types, 81 Fossils, 447 Fovea centralis, 336 Fresh-water habitat, 80 Fructose, 97 Fruit, 390 FSH, 396 Fuel, respiratory, 249 Fungi, 137 reproduction of, 375

Galactose, 97 Gamete, 356 Gametophyte, 377 Ganglion, 324 Gas exchange, 233 Gastric juice, 220 Gastrula, 400 Gel. 105 Gemma, 144 Genes, 33 cellular roles of, 293 definition of, 288 and evolution, 435 function of, 290 in heredity, 412 in protein synthesis, 269 recessive, 416 structure of, 288 Genetic drift, 436 Genome, 412 Genotype, 414 Genus, 120 Gills, 181, 189 Glands, 272 Glomerulus, 316 Glottis, 235 Glucose, 25, 97 in blood, 228 formation of, 211 Glycerin, 25, 98 Glycogen, 98, 226 Golden-brown algae, 128 Golgi bodies, 114 Gonads, 394 Grana, 206 Grassland, 81 Green algae, 127 Growth, 398 Guanine, 290 Guard cells, 159 Gymnosperms, 146 reproduction of, 384

Habitats, 75
Haploidy, 363
Hardy-Weinberg law, 435
Hatching, 393
Hearing, 340
Heart, 309
Heartwood, 155
Heat production, 266
Hemoglobin, 243
Herbaceous plants, 148
Herbivores, 164
Heredity, 411
Hermaphroditism, 362

Heterospory, 384 Heterotrophs, 197, 216 Heterozygosity, 416 Hominoids, 464 Homospory, 384 Homozygosity, 416 Hormones, of animals, 298 of plants, 296 types of, 301 Hornworts, 144 Host in parasitism, 72 Humus, 199 Hunger, 218, 219 Hydrogen, acceptor of, 248 in protoplasm, 95 transfer of, 253 Hydroponics, 199 Hyperparasitism, 71 Hypertonicity, 109 Hypha, 139 Hypothalamus, 219 Hypothesis, 5 Hypotonicity, 109

Ice ages, 86 Ichthyosaurs, 455 Independent assortment, 417 Induction, embryonic, 403 Information, 278 Ingestion, 218 Inhalation, 237 Inheritance, 411 Inorganic compounds, 25, 96 Insects, 182 Intermediate hosts, 73 Interneuron, 322 Internode, 155 Intestinal juice, 220 Intestine, 223 Intrathoracic space, 237 Ionization, 101 Iris, 334 Isotonicity, 109

Kelps, 130 Kidney, function of, 316 structure of, 315

Labyrinthodonts, 455 Lacteal, 226 Lactic acid, 255 Lactose, 97 Lamarck, 430 Laminarin, 130 Lamprey, 189 Larva, 393 Larynx, 234 Leaf. 159 Learning, 344 Lemur, 462 Lens, 334 Leucocyte, 307 Levels of organization, 48 LH. 396 Lichen, 140 Light, in photosynthesis, 208 production of, 267 Limulus, 184 Linear order, law of, 418 Linkage, genetic, 418 Lipase, 105, 220 Lipid, 98 Liver, 229 Liverworts, 144 Living, definition of, 47 Locomotion, 164 Lungs, 192, 237 Lycopsids, 145, 453 Lymph system, 226 Lymphocyte, 307

Malaria, 136 Maltose, 97 Mammals, 194 evolution of, 457 Man, characteristics of, 468 early history of, 467 evolution of, 458 status of, 468 Mastigophora, 133 Mating types, 361 Medulla oblongata, 238, 312, 343 Medusa, 170 Megaspore, 384 Meiosis, 362 Mendel, laws of, 413, 417 Menstruation, 397 Meristems, 151 Mesoderm, 167, 401 Mesogloea, 170 Mesophyll, 161 Mesozoic, 455

Metabolism, definition of, 44 Metamorphosis, 394 in insects, 185 Metaphase, 351 Metaphyta, 122 reproduction of, 377 Metazoa, 122 reproduction of, 392 Methane, 22 Microsome, 114, 270, 292 Microspore, 384 Migration, animal, 64 Millipedes, 185 Mimicry, 68 Minerals, 90, 96 Mitochondria, 114 in respiration, 247 Mitosis, 351 Modulator, 278 Molecules, 18 reproduction of, 350 Mollusks, 175 Monera, 35, 122 reproduction of, 371 Monkeys, 463 Monosaccharide, 97 Morphogenesis, 398 Mosses, 144 reproduction of, 379 Motor neurons, 322 Mountain building, 83 Mountain habitat, 83 Movement, 264 Mucosa, 223 Muscle action, 265 Mushrooms, 140, 376 Mutation, 30, 412, 425 Mutualism, 70 Mycelium, 139 Mycophyta, 138 Myelin, 322

Nasal passages, 234 Natural selection, 431 modern meaning of, 433 Neanderthal man, 467 Nekton, 76 Nephron, 316 Nerve impulse, 327 Nerves, 321 Nervous system, 320

Myxophyta, 136

Neural receptors, 330 Neuron, 321 Nicotinic acid, 254 Nitrates, 89 Nitrification, 90 Nitrogen, fixation of, 89 global cycle of, 89 in protoplasm, 95 Nodes, 155 Nonelectrolytes, 101 Nose, 333 Notochord, 188 Nucleic acid, 27, 99, 289 Nucleolus, 111 Nucleoprotein, 28, 99, 289 Nucleotide, 27, 99, 289 Nucleus, 35, 111 Nutrition, 29, 44

Ocean, 76 Ocean currents, 86 Oil, 98 Olfactory lobe, 334 Omnivores, 164 Open system, 84, 279 Optic lobe, 337 Optic nerve, 336 Order, taxonomic, 120 Ordovician, 452 Organ, 48 of Corti, 340 Organ systems, 52 Organic compounds, 25, 96 Organisms, 43 Osmosis, 108 in root, 200 Ovary, in animals, 361, 394 in plants, 388 Oviducts, 394 Ovulation, 397 Ovule, 385 Oxidation, 248, 251 Oxide, 41 Oxygen, 39 in breathing, 241 in protoplasm, 95 Oxygen cycle, 88 Oxygen debt, 256 Ozone, 39

Pace maker, 311

Paleozoic, 451 Pancreatic juice, 220 Parapodia, 180 Parasitism, 34, 36, 70 Parasympathetic nervous system, 325 Parenchyma, 151 Parthenogenesis, 59, 173 Passage cell, 157 Peck order, 64 Perennials, 148 Period, geologic, 447 Peripatus, 182 Peristalsis, 223 Permeability, 107 Permian, 454 Petal, 388 Petiole, 159 PGAL, 211 in respiration, 258 pH, 102 Phaeophytes, 130 Phase reversals, 105 Phenotype, 414 Phloem, 152, 204 Phosphates, 251 Phosphoglyceraldehyde, 211 Phosphorylation, 224, 252 Photolysis, 209 Photosynthesis, 37, 198 details of, 205 summary of, 214 Phrenic nerves, 239 Phycocyanin, 125, 131 Phycoerythrin, 125, 131 Phylum, 120 Pineal eve, 192 Pistil, 388 Pith, 152 Pithecanthropus, 467 Placenta, 406 Placoderms, 453 Plankton, 76 Plants, hormones of, 296 origin of, 38 reproduction of, 371 structure of, 119 Plasma membrane, 107 Plastids, 114, 206 Pleistocene, 466 Plesiosaurs, 455 Pleural membranes, 237 Polar body, 366 Pollen, 385

Pollen tube, 387 Pollination, 383 Polyp, 170 Polysaccharide, 27, 98 Population, 55 Postganglionic fiber, 326 Pre-Cambrian, 448 Preganglionic fiber, 326 Pregnancy, 397 Primates, 460 Procambium, 152 Progesterone, 397 Prophase, 351 Prosimians, 462 Protein, 27 specificity of, 99, 269 structure of, 98 Protein synthesis, 269 Proteinase, 105, 220 Protista, 35, 122, 125 reproduction of, 372 Protoplasm, 47 composition of, 95 Protozoa, 133 reproduction of, 377 Pseudocoelomates, 171 Pseudopods, 133 Psilopsids, 145, 452 Pteropsids, 145, 453 Pterosaurs, 455 Pulmonary vessels, 309 Pulse, 311 Pupa, 185 Pupil, 334 Purines, 25, 99 Pus. 307 Pyrimidines, 25, 99 Pyrrophytes, 131 Pyruvic acid, 255, 257

Races, human, 468
Radiata, 168
Radiolaria, 134
Rain forest, 81
Reactions, chemical, 20
Receptors, 278
neural, 330
Recessive genes, 416
Red algae, 131
Red corpuscles, 305
Reflex, 322
conditioned, 344

Regeneration, 355 Reproduction, 28, 45, 349 of cells, 351 gametic, 357 of organisms, 355 organs of, 361 sporulative, 356 vegetative, 356 Reproductive cells, 356 Reproductive system, 361 Reptiles, 193 evolution of, 455, 457 Respiration, 32, 44, 246 summary of, 260, 262 Response, 46, 277 Retina, 334, 336 Rhodophytes, 132 Riboflavin, 254 Ribose, 99 RNA, 99, 289 distribution of, 112 Rods, 336 Root, 156, 158 functioning of, 200 Rootcap, 156 Root hair, 157 Root pressure, 202, 203 Rotifers, 173 Roundworms, 174

Saccule, 339 Saliva, 220 Salt, definition of, 102 Saprophyte, 36, 216 Sapwood, 155 Sarcodina, 134 Satiety center, 219 Schizocoelomates, 175 Schizophyta, 123 Schwann sheath, 322 Science, nature of, 3 Sclera, 334 Sea, 76 Secondary growth, 153 Secretion, 272 Seed, 385 Seed plants, evolution of, 454 life cycle of, 383 Segregation, law of, 414 Self-fertilization, 362 Self-perpetuation, 44 Semicircular canals, 339

Sense organs, 330 Sensory neuron, 322 Sepal, 388 Sex. 358 function of, 360 in heredity, 412 inheritance of, 422 Sex cells, 356 Sex chromosomes, 422 Sex hormones, 395 Sieve tube, 153 Silurian, 453 Sinus node, 312 Sinuses, 234 Slime molds, 136 Smell, 333 Snails, 175 Society, 58, 63 Soil, 199 Sol, 105 Solution, 105 Somite, 189 Sorus, 381 Specialization, 51 Speciation, 55, 437 Species, 48, 55, 120 origin of, 437 Specificity, of enzymes, 104 of proteins, 99 Sperm, 356 Sperm duct, 394 Sphenopsids, 145, 453 Spicules, 168 Spiders, 185 Spinal cord, 341 Spindle, 351 Spirillum, 124 Sponges, 169 Sporangium, 376 Spore, 357 Sporophyte, 377 Sporozoa, 136 Squids, 178 Stamen, 388 Starch, 98, 213 Starfish, 186 Steady-state control, 45, 277 Stigma, 388 Stimulus, 45, 277 Sting cells, 169 Stomata, 148, 159 Stone age, 467

Semiherbaceous plants, 153

Subhumans, 465
Sucrose, 97
Sugar, 25, 97
Symbiosis, 69
Sympathetic chain ganglia, 325
Sympathetic nervous system, 325
Synapse, 322
Syncytium, 111
Synthesis, 21, 44
processes of, 268
of proteins, 269
Systole, 310

Taiga, 82

Tapeworms, 71 Tarsiers, 462 Taste, 332 Taxonomy, 119 Tear ducts, 235 Tectorial membrane, 340 Telophase, 351 Template hypothesis, 291 Temporal lobe, 341 Testis, 361, 394 Testosterone, 395 Thecodonts, 455 Theory, 8 Therapsids, 457 Thrombin, 308 Thymine, 290 Thyrotropic hormone, 300 Thyroxin, 261, 300 Tissue, 48 Tongue, 332 TPN, 254 Trachea, 234 Tracheal tubes, 182 Tracheophytes, 145 reproduction of, 380 Transduction, 424 Transformation, genetic, 425 Translocation, 205 Transpiration, 203 Trilobites, 452 Tube feet, 186 Tundra, 83 Tunicates, 189 Turnover, metabolic, 268 Twins, 400

Urea, 229

Ureter, 316 Urethra, 315 Urine, 317 Uterus, 394 Utricle, 339

Vacuoles, 114
Vagus nerve, 311
Variations, inheritable, 56, 412, 433
Vascular bundles, 152
Vasomotion, 314
Vegetative reproduction, 355
Veins, 241
in leaf, 158
Vena cava, 241, 309
Ventricles, 309
Vertebrates, 189
evolution of, 452

Villus, 223 Virus, 33, 70 Vision, 334, 337 Visual purple, 337 Vitamins, 295, 297 Vitreous humor, 334 Vocal cords, 236 Voice, 236

Water, 22 and climate, 85 properties of, 86 in protoplasm, 96 Water cycle, 88 Water-vascular system, 186 Watson-Crick model, 290 Wax. 98 White blood cells, 307 Winter hardening, 149 Wood, 154

X chromosomes, 422 Xanthophyll, 128, 206 Xylem, 152, 202

Y chromosomes, 423 Yolk, 404 Yolk sac, 405

Zooflagellates, 133 Zygospore, 359 Zygote, 357

.el

s pa

· A

DEPARTMENT OF SUM PHEN DERRHY SATINE BUILDING MIS SUMSET & DASTER WYENDE DUMSTON, WISSISSE

SUPPLEMENT

TO

Weisz, P. B., ELEMENTS OF BIOLOGY, McGraw-Hill,—Canadian Edition 1963

POINTS OF VIEW ON THE THEORY OF EVOLUTION

l by:

Subcommittee ent of Education Canada

pany the Text for Biology 30

April 1963

The many excellent qualities of ELEMENTS OF BIOLOGY by Dr. P. B. Weisz led to its recommendation as the basic text for the Biology 30 course. Dr. Weisz is a scientist of the highest repute, active in research and widely respected. He writes well and the book is up-to-date. He presents the fundamental biological principles which are required, and gives clear explanations of difficult material.

However, his treatment of the origins of life and its subsequent development may cause concern. It was felt that a supplement would be helpful in resolving difficulties which could arise as well as giving an opportunity for presenting other relevant information not given in the text. Dr. Weisz frequently warns readers that his explanations of the origins of life are speculations and that there is no concrete evidence yet available. But it is easy to lose sight of these qualifying statements. Students may retain a misleading impression that he is making dogmatic statements of fact. It is important to remember that the author's views are not the only

way to view these controversial topics.

The beginnings of life are necessarily shrouded in mystery. From a scientific standpoint neither scientists nor philosophers can make statements of fact. It is in the nature of the subject that we cannot prove how life began or exactly what happened so many millions of years ago. Dr. Weisz puts forward the ideas of some scientists, but there are other possibilities. You will notice that he states that science should not be concerned with nonscientific subjects. To most people the formation of the world was an act of special creation controlled by God. There is no evidence that it was not so, and some scientists as well as clergy and churchmen support this view. The origin of life is not a necessary part of the study of biology at this level. Religion and faith are personal matters beyond the scope of this course. In short the origin of life is no more relevant here than is life after death.

The theory of evolution, however, as distinct from the origin of life, is an integral part of biology today, and no adequate course can be presented without reference to it. Most denominations of Christianity have accepted the concept without prejudice to their faith. The theory of evolution states that complex organisms have arisen from simpler forms of life.

Some of the supporting evidence is presented in the text, but Dr. Weisz does not set out to give a comprehensive account. It is noteworthy that the latest research on cell structure (11, 15, 16), hormones, enzymes and blood chemistry, embryology (2), together with fresh fossil finds (6, 7, 27) and geological research (13, 18, 31), demonstrates the validity of the theory. However, scientists hold divergent views on the exact way in which all the important processes have come about. This is not difficult to understand when we consider the relatively short time for which research workers have had the benefits of technical aids to help them in this field. There are still some people who find the theory difficult to accept and feel they have sound reasons to support them. Dr. Weisz has not included questions often raised by interested students; they have been summarized below with brief comments.

1. The age of the earth

Evolution of new species proceeds so slowly that it is difficult to see positive evidence of it in a lifetime — or even within the recorded history of science. For life to have evolved in this way it is necessary that the earth be sufficiently old. Has there been sufficient time for the rise of complex organisms by natural means alone?

Age dating methods have been criticized (1, 4, 5) as giving too great an age for the earth (25), but the best available evidence affirms that a combination of two or more methods gives a very reliable estimate (10, 12, 14, 20, 21).

2. The incompleteness of the fossil record

Few fossils have yet been found which are older than the Cambrian period. It is impossible, at present, to trace a complete and consecutive story of the evolutionary development of any present day organisms. There are also unexplained extinctions followed by times of sudden increase in the numbers and kinds of living things (25, 26). Scientists believe these events will be explained satisfactorily by further research, but the fact remains that at the moment the evidence is not available. Dr. Weisz admits these inadequacies but seems to accord them insufficient weight. An alternative theory suggests that they are evidence of Divine planning, and that an overruling power has directed development of life throughout the ages. You may accept the theory you find convincing.

3. The development of the major groups of plants and animals

The development of species can be observed, but there is little concrete evidence of the radical changes necessary to develop new phyla. It is difficult to see how, in their early and presumably non-functional stages, developing structures can have had survival value and thus have been preserved and perfected.

4. Entropy and the second law of thermodynamics

The development of more complex forms from simpler types has been said to be contrary to the second law of thermodynamics; the law which expresses the observed facts of the reduction of the availability of energy. The expected trend would be one of deterioration and simplification. This is one of the aspects of life which is not yet explicable purely in terms of contemporary physics and chemistry, but some contemporary biologists feel that the law should not be applied here at all. It is here that we come back to the unresolved controversy between the mechanists and the vitalists. Mechanists believe that all the phenomena of living things will eventually be explicable in terms of physics and chemistry. Vitalists believe some other influence must be involved. The whole range of human experience of intangible factors bears witness to the fact that man, at least, is not simply a machine (3, 9, 17, 29).

5. The role of chance

Dr. Weisz states many times that chance alone is sufficient to explain evolution and adaptive radiation; others do not think so. It may depend on what we mean by chance. Some authors maintain that it was mathematically impossible for life either to have commenced fortuitously or to have developed by a series of chance occurrences. The experiments by Miller which resulted in the production of amino acids and other organic substances from the four chemical elements which were probably common in the earlier epochs of the earth are of great significance here. In only eight days by the use of an electrical spark some of the simpler molecules which form the basis of living things were produced. Such results weaken the theory of mathematical impossibility and suggest that this type of chance is simply probability of a different order of magnitude than that to which we are accustomed (28). Again, when we speak of natural selection the word itself implies the opposite of random behaviour or chance. This can be seen as another facet of the working of God's world.

There are other difficulties (25) but the student should not feel concerned about them. The course will offer a rich variety of experiences which should give insight into some of the principles involved and further reading is to be encouraged (19, 24, 30). A list of references will be found at the end of this supplement; most of the books are easily obtainable, many in cheap, paperback editions. Summaries of some of the more important scientific

papers are included.

Many scientists hold strong religious beliefs but accept the fact that evolution has been adequately demonstrated; they do not find the two beliefs incompatible (8, 23, 32). Philosophers, theologians, and eminent churchmen have thoroughly investigated the implications and found no obstacle to their faith. In fact, each concept may strengthen the other. The everyday miracle of life seems an inevitable accompaniment to a living God. To conclude we may quote a churchman, a scientist, and a saint.

In 1884 Dr. F. Temple, later Archbishop of Canterbury, who was one of the first Anglican churchmen to accept the theory of evolution, said: "It seems in itself something more majestic, something befitting Him to Whom a thousand years are as one day and one day as a thousand years, thus to impress His will once for all on this creation, and provide for all its countless variety by this one original impress, than by special acts of creation to be perpetually modifying what He had previously made."

Simpson, a noted scientist says, "Nevertheless, I take it as self-evident requiring no further special discussion, that evolution and *true* religion are compatible. It is also sufficiently clear that science alone does not reach all truths, plumb all mysteries, or exhaust all values and that the place and need for true religion are still very much with us."

St. Augustine held that "if we cannot resolve such a contradiction (between scientific and religious knowledge) we are to suspend judgment, not doubting either Holy Scripture or the results of human observation and reasoning; believing that it is possible, given sufficient knowledge and understanding, to reconcile the apparent contradiction."

REFERENCES

 Allan, R. S., 1948, "Geological correlation and palcoecology," Bull. Geol. Soc. America, 59, Jan., pp. 1-10.

It is argued that the criteria of correlation are logically vulnerable, and that the principles of stratigraphy need reformulating if the science is to regain its vitality and productiveness. Two possible lines of advance are indicated. The first, which may be called the paleoecological approach, involves the application of modern knowledge of sedimentation and ecology to stratigraphy and implies greater use of the facies concept. It is suggested second, that greater attention should be paid to the study of restricted groups of organisms as they evolve in time through strata of uniform lithology. Finally the possibility of linking lineage studies with facies-shift is pointed out.

*2. de Beer, Sir G., 1958, Embryos and Ancestors, Oxford University Press, xii + 197 pp.

*3. Blum, H. F., 1955, Time's Arrow and Evolution, University Press, Princetown, 2nd Ed., xi + 219 pp.

 Boyle, R. W., 1959, "Some geochemical considerations on lead-isotope dating of lead deposits," Economic Geology, 54, Jan.-Feb., pp. 130-135.

The validity of age determinations based on the lead-isotope ratios of galena or other lead minerals in deposits is questioned. A few simple examples are given to show that fractionation of lead isotopes in geochemical processes is probable. The geochemical processes through which lead has passed must be considered in detail before an age can be assigned to a lead deposit.

 Burling, R. L., 1952, "Determination of geologic time," Nucleonics 10, May, pp. 30-35.

The meaning of the term "age" is rather unclear, at least for metamorphic rocks and mechanical sediments. For an igneous rock or a chemical sediment, we hope to find the time back to its crystallization, a process which may have taken place in so short a time as to be regarded as an event. But has the rock been isolated since then? Age determination methods require that the sample has neither gained nor lost any of the parent, daughter, or intermediate element. Geochemical studies have attempted to select, for each method, the minerals least likely to have changed.

Lewis suggested that the earth's crust was formed by cosmic ray action on an Iron-Nickel core. Although the effect of cosmic rays on abundances of elements used in age determination is not that great, it should be considered. Brajnikov suggests the fission of Uranium by neutrons of cosmic-ray or terrestrial origin as a possible source of error in Lead ages.

Another questionable assumption is that the material from which the sample was formed was of the same isotopic makeup as the average for the whole crust of the earth. Actually the parent material may have had a complex history

of isolation, remelting, contamination, reseparation, etc. Thus even in specimens unaltered since their last crystallizations, this isotopic constitution of an element having radiogenic isotopes might be characteristic of an age anywhere between that since the last isolation, and that since the material first solidified from a fluid outer shell of the earth.

When Uranium or Thorium is the parent element the methods require the assumption that the sample contained, at the time of its isolation, no nonequilibrium amounts of any radio elements intermediate between parent and the end product, Lead. There exist minerals for which this is not true as proven by Henderson's discovery of "fossil" pleochroic halos that correspond to decay of hydrothermally deposited intermediates, by Schlundt's work on the Radium content of Yellowstone tufas, and by the work of Piggot and Urry and Pettersson on deep sea sediments. (PARTIAL SUMMARY).

 Clark, W. E. le Gros., 1960, History of the Primates, an introduction to a study of fossil man, British Museum (Natural History) 7th Ed., 119 pp.

*7. Colbert, E. H., 1951, The Dinosaur Book, the ruling reptiles and their relatives, McGraw-Hill, New York, 156 pp.

*8. Dobzhansky, T., 1962, Mankind Evolving, Yale University Press, xiii + 381 pp.

9. Eddington, A. S., 1928, The Nature of the Physical World, Cambridge University Press, xix + 361 pp.

 Faul, H., (Editor), 1954, Nuclear Geology; A symposium on nuclear phenomena in the earth sciences, John Wiley and Sons, New York, xvii + 414 pp.

 Flanagan, D., (Editor), 1955, The Physics and Chemistry of Life, A Scientific American book, Simon and Schuster, New York, 11 + 270 pp.

 Folinsbee, R. E., Baadsgaard, H., and Lipson, J., 1960, "Potassium-Argon time scale," *International Geological Congress XXI*, Session III, Pre-Quaternary Absolute Age Determination, pp. 7-17.

At certain key points on the paleontologic time scale it has been possible to collect minerals of known biostratigraphic age amenable to potassium-argon dating. Late Cretaceous (Maestrichtian) sanidines from a dinosaur-bearing bentonite bed give an age of 66 million years, mica from the same horizon ages of 75 and 79 million years. Upper Cretaceous (Campanian) volcanic bentonites give biotite ages of 68 and 82 million years. A mid-Cretaceous sanidine is 94 million years old, but middle Albian biotite is 114 and 119 million years old. This suggests argon leakage from sanidine. Potassium-argon ages for Cretaceous and Jurassic glauconites are variable, usually younger than correlative biotite or sanidine ages. Sanidine from an Exshaw shale bentonite which marks the Devonian-Mississippian contact, gives ages of 242 and 250 million years, figures in agreement with Holmes time scale. A well ordered lower Cambrian glauconite



Lower (early), clearly does not, on the basis of biostratigraphic considerations, represent equal or even similar time intervals. The geological time scale has developed to the place where it can be used for correlation problems in paleontology, orogeny, and mineralization. Although much remains to be done, particularly in the lower Paleozoic, enough has been accomplished to demonstrate the potential accuracy that may ultimately be attained and the new objectivity that has been introduced in the time dimension in geology. (PARTIAL SUMMARY).

- *22. Lack, D., 1957, Evolutionary Theory and Christian Belief, Methuen and Co., London, 128 pp.
- *23. Lecomte du Nouy, Pierre, 1947, Human Destiny, Longmans Green, N.Y. and London, xix + 289 pp.
- 24. Moment, G. B., 1958, General Zoology, Houghton Mifflin, Riverside Press, Cambridge, Mass., 632 pp.
- *25. Morris, H. M., and Whitcomb, J. C., (Title page: Whitcomb & Morris), *The Genesis Flood*, 1961, The Presbyterian and Reformed Publishing Co., Philadelphia, xxv + 518 pp.
- Newell, N. D., 1963, "Crises in the history of life," Scientific American, 208, Feb., pp. 76-92.

It might be argued that nothing less than the complete destruction of a habitat would be required to eliminate a world-wide community of organisms. This, however, may not be necessary. After thousands of years of mutual accommodation, the various organisms of a biological community acquire a high order of compatibility until a nearly steady state is achieved. Each species plays its own role in the life of the community, supplying shelter, food, chemical conditioners or some other resource in kind and amount needed by its neighbors. Consequently any changes involving evolution or extinction of species, or the successful entrance of new elements into the community, will affect the associated organisms in varying degrees and result in a wave of adjustments. The strength of the bonds of interdependence, of course, varies with species, but the health and welfare of a community commonly depend on a comparatively small number of key species low in the community pyramid; the extinction of any of these is sure to affect adversely many others. Reduction and fragmentation of some major habitats, accompanied by moderate changes in climate and resulting shrinkage of populations, may have resulted in extinction of key species not necessarily represented in the fossil record. Disappearance of any species low in the pyramid of community organization, as, for example, a primary food plant, could lead directly to the extinction of many ecologically dependent species higher in the scale. Because of this interdependence of organisms a wave of extinction originating in a shrinking coastal habitat might extend to more distant habitats of the continental interior and to the waters of the open sea. This theory, in its essence long favored by geologists but still to be fully developed, provides an explanation of the common, although not invariable, parallelism between times of wide-spread emergence of the continents from the seas and episodes of mass extinction that closed many of the chapters of geological history.

- 27. Oakley, K. P., and Muir-Wood, H. M., 1959, *The Succession of Life through Geological Time*, British Museum (Natural History) London, vii + 94 pp.
- *28. Simpson, G. C., 1949, *The Meaning of Evolution*, Yale University Press, Revised and abridged, Mentor Books New York, 1951, 192 pp.
- *29. Simpson, G. G., Pittendrigh, C. S., and Tiffany, L. H., 1957, Life — An introduction to biology, Harcourt, Brace and Co., New York, xiv + 845 pp.
- Smith, J. M., 1958, The Theory of Evolution, Penguin Books, London, 320 pp.
- Stutzer, O., Geology of Coal, translated and revised by A. C. Noe, 1940, University of Chicago Press, viii + 461.
- *32. Teilhard de Chardin, P., 1959, The Phenomenon of Man, Wm. Collins Sons & Co. Ltd., London, 320 pp.
- *Available in the Extension Library, University of Alberta in Edmonton.















Date Due

Dute Due			
2 10 12	W. IT. KU	EDUC FE	12.41
	14	1,24.64.	a mark
EDUC S 2	4'73	WHITE T	6 77
SEP 24 RI	TIIRN F	EB 4 6 11	IURM
	5/7/	با:	
DEC 7 R	ETURN	(1.2) _ 1	7 3 19
	7'74 ETURÎN R	ETURNED	R 20 '78
בית הווז	3094	Bys. will p	R 22'78
DEC 6 F	ETURN	ETURNED?	14'78
	. w/s -		100
JAN 30	HETURN	OCT 1 7	RETURN
EVILL AT 1	70 10	بروان مشيا تا	3 6 24
Control State Co	RETURN		
AUG 1 6 F	KE IKEL	MAN JAN	2 7 1984
4		EDUC FEE	3 '84
607 97	RETURN	red 3	TEIUKN
	j	DUE	NOV 16'84
= 11,00=	4 77	NOV	44'84
EURE TO	178	NOW ZA	d sales UTIM

OH 308=5 W43 WEISZ PAUL B 1921= ELEMENTS OF BIOLOGY

39390104 CURR HIST



